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TEMPLE CLAYTON, CHEMIST AND AMATEUR BOTANIST, 1914–1978

BERNICE G. SCHUBERT

THE FIELDS of natural history and botany have always had among their ranks rather large numbers of interested and enthusiastic amateurs. In botany, at least, these people have devoted themselves whole-heartedly and often in a most professional manner to a pursuit that was actually a hobby, not the effort from which they derived their livelihood. In the past and even now, many amateurs have been and are much concerned with monocotyledonous plants, especially members of such families as the Bromeliaceae, Liliaceae, and Orchidaceae—all taxonomically and horticulturally difficult families with species scattered in often remote, hard-to-reach, tropical areas. Temple Clayton was one of those dedicated amateurs and had a tremendous interest in the Dioscoreaceae, or family of the true (tropical) yams.

Born in Andover, New Hampshire, on August 19, 1914, Temple Clayton died at White Bear Lake, Minnesota, on November 10, 1978. His early schooling (1927–1931) was at the Tilton Preparatory School, Tilton, New Hampshire. From there he went to Cornell University, where he majored in chemistry and received the bachelor of chemistry degree in 1935. He then went to the New York City area, where, while working as a chemist for various companies[1] and teaching chemistry,[2] he also did graduate work at Columbia University, receiving the M.A. degree in 1941. From June, 1944, to August, 1954, Mr. Clayton was employed as a group leader by the Schering Corporation, a pharmaceutical firm in New Jersey with interests in natural products. Through his work involving chemical constituents of the underground parts of various species of *Dioscorea,* he became interested in the plant sources. (He had earlier

[1]September, 1935–June, 1936, as research chemist for Kessler Chemical Corp.; August, 1936–February, 1937, as chemist for Carleton Ellis.

[2]First (February, 1937–June, 1938) at Newark College of Engineering, then (September, 1938–June, 1944) at Cooper Union.

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TEMPLE CLAYTON
1914–1978

become interested in plants through the influence of his uncle, the late A. Le Roy Andrews, professor of Germanic philology at Cornell, but well known for his interest in plants and as an American authority on mosses, particularly the genus *Sphagnum*.) As an intellectual adjunct to his chemical work, Temple Clayton plunged from a rather casual concern with local flora to a serious study of a botanically difficult plant family. He pursued this activity mostly on his own time, but with travel support from the Schering Corporation, botanical support from the New York Botanical Garden, and some technical assistance and serious interest from the U. S. Department of Agriculture.

In November, 1954, Temple Clayton went to work for the 3M (Minnesota Mining and Manufacturing) Company, where from the time he arrived until July, 1962, he worked in the Central Research Laboratories, first as a literature chemist then as a patent liaison. From August, 1962, until his death in 1978,

Specimens of Dioscoreaceae
From the Collections of Temple Clayton
Presented to the Arnold Arboretum of
Harvard University by the
Herbarium, Department of Botany,
University of Minnesota, St. Paul, 1979

Photographs of Dioscoreaceae
From the Collections of Temple Clayton
Presented to the Arnold Arboretum of
Harvard University by the
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University of Minnesota, St. Paul, 1979

Above: label to be used on Temple Clayton's herbarium specimens. Below: label to be used on his photographs.

he was employed as a patent agent in the Office of Patent Counsel of 3M. Mr. Clayton was admitted to practice before the United States Patent and Trademark Office, and he was a member of the Minnesota Patent and Trademark Law Association.[3]

During his 24 years in Minnesota, Mr. Clayton continued his interest in the Dioscoreaceae, supported by the encouragement of Gerald Ownbey, professor of botany and curator of the herbarium at the University of Minnesota, St. Paul. So far as I can tell, it was during this period that Temple Clayton formulated most of his ideas about the reorganization of the family Dioscoreaceae—work for the most part written up, sometimes roughly and sometimes in more finished form, but none of it published. He had, however, annotated specimens in many herbaria with unpublished names.

He photographed every specimen he had on loan from European herbaria, proposed a whole new classification for the family Dioscoreaceae and its components, wrote detailed descriptions for a large number of new taxa at various levels, and made sketches illustrating significant characters of the plants. He accumulated a vast bibliography, a good study collection of specimens, and a knowledge of theoretical approaches to taxonomic matters that was, to say the least, surprising.

At Temple Clayton's death, all the materials were given to the herbarium of the Department of Botany, University of Minnesota, St. Paul, by his wife, Emma G. Clayton. However, Professor Ownbey thought that the facilities and area of specialization there were not the best for materials concerned with an

[3]From a letter of Mr. Donald C. Gipple, senior patent attorney, 3M Co., March 1, 1982.

important group of tropical plants, and they were transferred to the Arnold Arboretum of Harvard University in 1979. Organizing the specimens and photographs to make them easily available and most useful has been a rather lengthy process, due to lack of continuous time, not lack of interest. The specimens (some mounted and some unmounted; some determined, some named as new, and some sterile and unidentifiable or represented by cultivated material grown by the U. S. Department of Agriculture) have been inventoried. Before being mounted, each specimen and photograph will have a special label affixed indicating the source and date of the gift. Duplicates will be made available to institutions whose collections were studied, as well as those with special interest in the Dioscoreaceae.

The acquisition of the Temple Clayton dioscoreaceous reliquiae has proven to be an interesting and somewhat awesome experience. The items making up the collection comprise the results of about 30 years of devoted attention to a fascinating avocation for which Mr. Clayton was basically untrained. I make this last remark not in a sense of judgment, which is not my purpose here, but in a sense of wonder that he accomplished such a large amount of time-consuming work and made so many meticulous observations in spare hours.

Although the materials were turned over with "no strings attached," Temple Clayton's friends and colleagues in Minnesota hoped that something publishable might be found that could bear his name as author. There is little doubt that some of the species he indicated as new, and for which he wrote descriptions and annotated specimens, were indeed undescribed. To be as certain as possible, I enlisted the collaboration of Dr. Franklin Ayala, director of the Herbarium Amazonense, Iquitos, Peru, and also a student of Dioscoreaceae, to study some of the material with me. In the short time we had to work together, we chose four species from among those left by Temple Clayton; these will be published in a separate paper.

My acquaintance with Temple Clayton extended over a long period, starting before he left New Jersey for Minnesota, when he was studying plant material at the New York Botanical Garden and visiting the (then-called) Plant Industry Station of the U.S.D.A. at Beltsville, Maryland, to see some of his own material growing in the greenhouses. He was generous about sharing with me materials he had on loan from Europe, as well as information as he acquired it on Dioscoreaceae. He was an interesting, enthusiastic person, very serious about his chief interests, with an amiable personality and boundless energy. I trust that my colleagues and I will be able to do justice to some of the results he left unpublished.

For the photograph and other useful information I am indebted to Mrs. Emma G. Clayton; for other data, to Mr. Donald C. Gipple, of the 3M Company; and for the privilege of having the material presented to the Arnold Arboretum of Harvard University for my study, to Dr. Gerald B. Ownbey.

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THE ZINGIBERALES (CANNACEAE, MARANTACEAE, AND ZINGIBERACEAE) IN THE SOUTHEASTERN UNITED STATES[1]

GEORGE K. ROGERS

THE ORDER ZINGIBERALES (Scitamineae, Scitaminales) is clearly delimited and is universally accepted as a natural group of four to eight families, depending on the ranks assigned to some of its chief components. Emphasizing anatomical evidence in addition to morphology, Tomlinson (1962, 1969) advocated recognition of Zingiberaceae, Costaceae (often included in Zingiberaceae), Marantaceae, Cannaceae, Musaceae, Lowiaceae, Heliconiaceae, and Strelitziaceae (the last three often included in Musaceae). Other recent authors differ as to which of the segregates are chosen for elevation to the rank of family. Zingiberaceae, Cannaceae, and Marantaceae are represented in the southeastern United States by a small number of indigenous and introduced species.

Transformation of stamens into sterile staminodes is a well-known trend bearing on the interrelationships of the families of Zingiberales. The Musaceae

[1]Prepared for the Generic Flora of the Southeastern United States, a long-term project of the Arnold Arboretum currently made possible through the support of the National Science Foundation under grants BSR-8111520 to Harvard University (Carroll E. Wood, Jr., Arnold Arboretum, principal investigator) and BSR-8303100 to the University of the State of New York (Norton G. Miller, New York Biological Survey, principal investigator). This treatment, prepared under BSR-8111520, is the 101st in the series. It follows the format established in the first paper (Jour. Arnold Arb. **29:** 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets [ ]. References that I have not verified are marked with an asterisk.

Special thanks are due to those who responded to my requests for information on Zingiberales. All of the replies were thoughtful and truly helpful. I am indebted in this connection to Daniel F. Austin, the late George N. Avery, Carl W. Campbell, Robert K. Godfrey, Richard A. Howard, Walter S. Judd, Julia F. Morton, Ghillean T. Prance, and John W. Thieret, as well as to the additional authorities consulted by some of them. Figure 1 was drawn by Margaret van Montfrans using dissections prepared by Carroll Wood from a plant cultivated by Theodore Schultz, in Boston, Massachusetts. Karen Stoutsenberger, supervised by Kenneth Robertson and Carroll Wood, prepared Figure 2 from a living specimen collected in Florida by Carroll Wood and cultivated at the Arnold Arboretum in Jamaica Plain. Figures 3 and 4 are also the work of Karen Stoutsenberger, directed by Carroll Wood. Materials for these figures were collected or otherwise provided by Manuel Flores, Robert Godfrey, Richard Howard, Peter Stevens, and Carroll Wood. Stephen Spongberg and Carroll Wood are thanked for their careful reviews of the manuscript. Elizabeth Schmidt's editorial improvements are gratefully acknowledged. Barbara Nimblett substantially expedited preparation of the bibliographic entries.

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and its segregates have five or rarely six fertile stamens, a condition that invites interpretation as primitive (see pertinent discussion in Dahlgren). Zingiberaceae *sensu lato*, Marantaceae, and Cannaceae have only one fertile stamen, with the others developing as petaloid staminodes or sometimes absent; in the two latter families half of the fertile stamen is petallike. Comparison of the families is provided in the key below, where further ties between the Cannaceae and Marantaceae—and characters separating these families along with Zingiberaceae from Musaceae *sensu lato*—are enumerated. Inviting as it may be to extrapolate a phylogenetic scheme from the characters in the key, the cladistic relationships of the eight putative families of the Zingiberales are obscured by contradictory characters, uncertainties surrounding homologies of apparent similarities (e.g., the diverse "arils" and chalazal inclusions in the seeds), and insufficient sampling for several characters. Phylogeny within the order and problems with its assessment were discussed by Tomlinson (1962), who suggested Strelitziaceae as the least specialized family.

The best taxonomic position for the Zingiberales is debatable. Hutchinson derived them from the Bromeliales (one family), and these from Commelinales. Bromeliales and Zingiberales were thought by Takhtajan to have a common origin from lilialean stock; Cronquist (1978, 1981) united the two orders as subclass Zingiberidae. In Thorne's scheme, the Zingiberales were placed in superorder Commeliniflorae along with the Bromeliaceae (a member of the Commelinales). Superorder Zingiberiflorae (containing only the Zingiberales) was hypothesized by Dahlgren (p. 140) to have arisen from liliiflorean ancestors on a "pro-commeliniflorean-zingiberiflorean-bromeliiflorean branch."

A prevalent concern in the literature on Zingiberales is interpretation of their androecia in terms of a presumably ancestral arrangement with three stamens in an antesepalous outer cycle alternating with three others in an antepetalous inner cycle. Interpretations involving patterns of venation, and positional, teratological, developmental, and anatomical evidence bearing on this matter are reviewed in Costerus (1916a, 1916b, 1916c), Eichler (1873; 1884, under Marantaceae), Holttum (1950, under Zingiberaceae), Kirchoff (1983b), Rao *et al.*, and Schachner. A brief overview follows.

In the relatively uncontroversial Marantaceae the inner cycle of the androecium probably includes the fertile stamen with its lateral appendage, the cucullate staminode, and the callose staminode (synonymy for these floral parts is provided with the family description). The outer cycle must then be represented by one (usually) or two petallike staminodes, with the third member suppressed. Support for this widely accepted interpretation appears in developmental studies by Eichler (1884) and Kirchoff (1983b): both observed a primordial ring, positioned above the calyx, which splits tangentially in each of the three alternisepalous positions to yield altogether three petals to the outside and three members of the androecium (fertile stamen, cucullate staminode, and callose staminode) to the inside. Primordia for the remaining (outer) staminodes are antesepalous. Eichler found floral vasculature to corroborate the developmental evidence (see also Tilak & Pai, 1966, 1968).

On the basis of developmental similarities, studies of Eichler (1884) and Kirchoff (1983b) agree further that flowers of Cannaceae are fundamentally as

described above for Marantaceae, with one or two (or sometimes no) petallike staminodes representing the outer androecial cycle, and with the labellum, one petallike staminode, and the fertile stamen (or no) as the inner cycle. According to both authors, these structures are homologous with the marantaceous cucullate staminode, callose staminode, and fertile stamen, respectively. Marantaceae and Cannaceae have been said to differ in the sequence of initiation of calyx lobes: those of Cannaceae spiraled in the same direction as the corolla and androecium vs. the spirals opposed in Marantaceae. However, Costerus (1916c) observed in a species of *Canna* many instances in which the calyx and corolla formed opposite spirals.

Few contemporary observers would dispute that in the Zingiberaceae the inner staminal cycle is represented by two staminodes connate to form the labellum plus the separate fertile stamen; clearly the outer cycle is sometimes (e.g., in Hedychieae) manifest as two free petaloid staminodes. However, the fate of the third (median) outer staminode, which is never unambiguously apparent, and the whereabouts of the two lateral staminodes when they are not obvious, remain problematic. Authors commonly consider fusions with the labellum as potentially accounting especially for the recondite median staminode (e.g., see Costerus, 1916b; Gregory), and sometimes for all three outer staminodes. Pai (1965b, 1966), however, stressed vascular evidence, while arguing in favor of the "classical view" that the labellum in at least some Zingiberaceae involves only the two inner staminodes. At the other extreme, the labellum composed of all five staminodes has been numbered among the characters that distinguish *Costus* L. (-oideae, -aceae) (see Costerus, 1916b; Cronquist, 1981; Holttum, 1950; Loesener; Maas, 1972; Schachner; Thompson, a contrary conclusion; Tomlinson, 1956; several of the references in this and the following paragraph are listed under Zingiberaceae). This distinction is best regarded as open to refinement. In some genera of Zingiberoideae, the lateral staminodes are ostensibly manifest as large or small lobes or teeth on the labellum.

Dampening the temptation to regard all lobes on the labellum in Zingiberaceae as adnate outer staminodes, Burtt (1972) pointed out that the elaborately lobed labellum of some orchids is homologous with a single perianth member. He also observed that the number of lobes on the zingiberaceous labellum in some cases exceeds the number of missing staminal components. Moreover, in *Hedychium coronarium,* in which the lateral staminodes are strongly and distinctly developed, the labellum sometimes has lateral lobes.

Contrary to interpretations of the epigynous glands of Zingiberaceae as modified stamens or styles, these nectaries have been shown to be vascularized carpellary outgrowths that range in position from being enclosed within apically open ovarian cavities in Costoideae to rising vertically above the summit of the ovary in Zingiberoideae (Pai, 1966; Rao).

General description of Zingiberales:

Small to arborescent, perennial, rhizomatous, mostly terrestrial herbs typically of moist tropical habitats. Hairs mostly unicellular. Leaves usually pet-

iolate, with sheathing bases (these often forming a pseudostem around a feeble true stem); blade entire, rolled in the bud, with a multistranded midrib region and many pinnate-parallel, lateral nerves; leaf axis usually with septate air canals. Inflorescences often with large, folded to spathelike, colorful primary bracts. Flowers usually perfect, zygomorphic or asymmetric, typically showy. Sepals 3, unlike the petals; petals 3, often unequal. Androecium the showiest portion of the flower (in our families), arranged fundamentally in 2 trimerous cycles; fertile stamen 1 [or 5 or 6], when 1 the flower with showy staminodes, these diverse in number, form, arrangement, and fusions, usually showier than the perianth. Gynoecium 3-carpellate, syncarpous and basically 3-locular (2 locules sometimes aborting), with 1 to many ovules per locule, ovary inferior [or flowers perigynous], style single. Seed with a specialized region of dehiscence, often operculate, usually with a micropylar collar, usually arillate (or with arillike emergences from the funiculus).

KEY TO THE FAMILIES AND GENERA OF ZINGIBERALES IN THE SOUTHEASTERN UNITED STATES[2]

A. Functional stamens 5 [or 6]; raphide-sacs present; guard cells with the inner and outer ledges equal. MUSACEAE (plants often of treelike appearance and size, with lateral buds opposite the leaves in *Musa*). . . . . [*Musa*.[3]]

A. Functional stamen 1; raphide-sacs absent; guard cells with the inner and outer ledges unequal (except in Cannaceae).

B. Leaf sheaths ligulate (FIGURE 1, b); flowers zygomorphic; sepals connate into a tube usually slit along 1 side (FIGURE 1, g); sterile staminodes represented by a usually broad labellum composed of 2 or more fused staminodes (the dual nature not readily evident) flanked by and sometimes adnate to 2 petallike to much reduced (to not detectable) lateral staminodes; anther with 2 locules, the style lying between them (FIGURE 1, h), on a nonpetaloid filament; pollen not deposited onto style in bud; nectaries vascularized emergences of carpellary tissue [or sometimes concealed in cavities]; endosperm development helobial. ZINGIBERACEAE.

C. Lateral staminodes strongly developed and petallike (FIGURE 1, g); labellum more or less flat (not troughlike), white to yellowish or marked with yellow; corolla tube several centimeters long; none of petals hoodlike. . . . . 1. *Hedychium*.

C. Lateral staminodes not apparent or reduced to small teeth; labellum troughlike, yellowish (especially toward the margin) or white, with reddish markings (especially toward the center); corolla tube to ca. 1 cm long; 1 petal hoodlike and facing labellum. . . . . [*Alpinia*.[4]]

B. Leaf sheaths without ligules (sometimes auriculate); flowers asymmetric; sepals distinct; sterile staminodes variously arranged but all distinct (except for basal

[2]For embryological comparisons of these families, see Panchaksharappa (under Zingiberaceae).

[3]Species of *Musa* L. are sometimes found growing outside of cultivation in Florida (and, according to Small, in Louisiana). Such occurrences appear to result usually, if not always, from persistence after cultivation, from rhizomatous spreading, or from inadvertent distribution by humans. Available evidence does not confirm bananas as truly naturalized components of the flora of the southeastern United States (see Black & Black, Lakela & Craighead, Long & Lakela, Melvill, Poppleton *et al.*, Thieret, Ward, Wunderlin, and acknowledgments in footnote 1).

[4]For comments on *Alpinia* Roxb., nom. cons., in the southeastern United States, see Zingiberaceae.

fusions); anther with 1 locule, the remainder of stamen petaloid or partly so; pollen deposited onto style in bud; nectaries septal; endosperm development nuclear.

D. Petioles not pulvinate at apex; stem with mucilage canals; staminodes consisting of a labellum and [0 or] 2 or 3 petallike staminodes (none of these hoodlike or appendaged) (FIGURE 2, d, e); style more or less petaloid, not curling inward, the region of pollen deposition not specialized, the stigma apical and marginal (FIGURE 2, k); gynoecium 3-locular, with many ovules per locule; seed opening by a slit, without canals in the (mostly chalazal) nutritive tissue; embryo straight; flowers single or in homodromous pairs. CANNACEAE. ..... 1. *Canna.*

D. Petioles pulvinate at apex; stem without mucilage canals; staminodes consisting of an appendaged, pouchlike "cucullate" staminode (FIGURE 3, g) enclosing the style before pollination, a hoodlike "callose" staminode (FIGURE 3, h), and 1 or 2 petallike staminodes; style not petaloid, curling rapidly inward when dislodged and effecting pollination, with a specialized region of pollen deposition (FIGURE 3, k-13), the stigma in a cleft (FIGURE 3, k-14); gynoecium unilocular (in ours), with 1 ovule per locule; seed operculate, with 1 or 2 canals in the (nucellar) nutritive tissue; embryo bent; flowers in mirror-image (antidromous) pairs (this not always conspicuous in *Maranta*). MARANTACEAE.

E. Petals distinct or nearly so; cucullate staminode with 2 appendages (FIGURE 3, g); outer petaloid staminode 1 (FIGURE 3, f); stigmatic cleft with a bifid rim projecting back into the flower (FIGURE 3, i–k); axes of flower pairs condensed (flowers of a pair borne tightly side by side; FIGURE 3, b); canal in seed forked at the base (in effect 2 canals). ..... 1. *Thalia.*

E. Petals connate into a tube; cucullate staminode with 1 appendage; outer petaloid staminodes 2; stigmatic cleft more or less funnel shaped; axes of flower pairs elongate; canal in seed forked only at the apex. ..... 2. *Maranta.*

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MAHANTY, H. K. A cytological study of the Zingiberales with special reference to their taxonomy. Cytologia **35:** 13–49. 1970. [Includes brief review of cytological literature, idiograms, drawings and photos of chromosomes, tables of chromosome numbers, and discussion of subdivision of Musaceae *sensu lato*; suggests that *x* ultimately = 11 in Zingiberales.]

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cludes details of many aspects of ovules, seeds, and embryos, especially useful in connection with the operculum and collar; embryological characters set Cannaceae apart from other Zingiberales.]

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MORTON, J. F. Pestiferous spread of many ornamental and fruit species in South Florida. Proc. Florida State Hort. Soc. **89:** 348–353. 1976. [*Alpinia speciosa*, *Canna indica*, *Hedychium coronarium*, *Maranta arundinacea*, 351, 352.]

———. Atlas of medicinal plants of Middle America. xxviii + 1420 pp. Springfield, Illinois. 1981. [*Canna coccinea*, *C. edulis*, *C. indica*, 111, 112; *Maranta arundinacea*, 113; Zingiberaceae, 103–107 (Costaceae, 108–110).]

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PERRY, L. M. (with the assistance of JUDITH METZGER). Medicinal plants of East and Southeast Asia: attributed properties and uses. x + 620 pp. Cambridge, Massachusetts, & London. 1980. [Cannaceae, 68; Marantaceae, 257; Zingiberaceae, 436–444; *Hedychium coronarium* and other species of *Hedychium*, 441, 442.]

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———, H. KARNIK, & K. GUPTE. The floral anatomy of some Scitamineae—part I. Jour. Indian Bot. Soc. **33:** 118–147. 1954. [*Hedychium coronarium* and 3 other species of Zingiberaceae; labellum probably a double structure belonging to the inner whorl.]

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RICKETT, H. W. Wild flowers of the United States. Vol. 2. The southeastern states. Part 1. x + 322 pp. New York. 1967. [Cannaceae, Marantaceae, Zingiberaceae, 91–93; color photos of *Hedychium coronarium, Canna flaccida, C.* × *generalis, Thalia geniculata*.]

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SCHERMERHORN, J. W., & M. W. QUIMBY, eds. The Lynn index, a bibliography of phytochemistry. Monograph III. Order, Scitamineae including the following families: Cannaceae, Marantaceae, Musaceae, Zingiberaceae; Order, Microspermae including the following family: Orchidaceae. 32 pp. Boston. 1958.

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SKUTCH, A. F. Unrolling of leaves of *Musa sapientum* and some related plants and their reactions to environmental aridity. Bot. Gaz. **90:** 337–365. 1930. [Cannaceae, Marantaceae (*Calathea*), 360–363.]

SMALL, J. K. Manual of the southeastern flora. xxii + 1554 pp. New York. 1933. (Reprinted, Chapel Hill, North Carolina. 1961.) [Scitaminales, 358–362; *Musa sapientum, M. Cavendishii, Canna flaccida, C. indica, Languas speciosa* (*Alpinia Zerumbet*), *Maranta arundinacea, Thalia dealbata, T. geniculata, Hedychium* "*coronatum.*"]

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THIERET, J. W. Checklist of the vascular flora of Louisiana. Part I. Ferns and fern allies, gymnosperms, and monocotyledons. Lafayette Nat. Hist. Mus. Tech. Bull. **2.** ii + 48 pp. 1972. [*Canna flaccida, C. glauca, C. indica, Thalia dealbata*, 37; *Musa* not listed.]

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THORNE, R. F. Proposed new realignments in the angiosperms. Nordic Jour. Bot. **3:** 85–117. 1983. [Zingiberales, 111; suborders Musineae and Zingiberineae.]

TILAK, V. D., & R. M. PAI. Studies in the floral morphology of the Marantaceae. I. Vascular anatomy of the flower of *Schumannianthus virgatus* Rolfe, with special reference to the labellum. Canad. Jour. Bot. **44:** 1365–1370. 1966. II. Vascular anatomy of the flower in two species of the genus *Phrynium* Willd. Proc. Indian Acad. Sci. **68B:** 240–249. 1968. III. Vascular anatomy of some species of the genus *Calathea*. Marathwada Univ. Jour. Sci. **2:** 31–41. 1970.*

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VENKATASUBBAN, K. R. A preliminary survey of chromosome numbers in Scitamineae of Bentham and Hooker. Proc. Indian Acad. Sci. **23B:** 281–300. 1946. [Most of the species listed as *Maranta* do not belong to this genus, if their epithets are correctly applied.]

WARD, D. B. Checklist of the vascular flora of Florida. Part 1. Univ. Florida Agr. Exp. Sta. Tech. Bull. **726:** 1–72. 1968. [*Musa acuminata* (*M. Cavendishii*), *M. paradisiaca* (*M. sapientum*), *Alpinia speciosa, Hedychium coronarium, Canna edulis, C. flaccida, C. indica, Maranta arundinacea, Thalia geniculata*, 56, 57.]

WILLIAMS, C. A., & J. B. HARBORNE. The leaf flavonoids of the Zingiberales. Biochem. Syst. Ecol. **5:** 221–229. 1977. [Zingiberales very much neglected from the chemical viewpoint; flavonoid evidence shows limited similarities to Bromeliales and "Fluviales"; includes table comparing families for leaf flavonoids; Cannaceae poor in flavonoids (based partly on second-hand reports, with cyanidin 3-rutinoside, quercetin, kaempferol); Marantaceae with "all classes of flavonoid constituent," delphinidin 3-rutinoside possibly common in leaves of Marantaceae but unknown in Zingiberaceae; *Maranta* with both flavones and flavonols; *Thalia dealbata* (from

other literature) with quercetin, cyanidin; Zingiberaceae with proanthocyanidins, kaempferol, quercetin, myricetin, isorhamnetin, syringetin—the last 3 flavonols mostly restricted to Hedychieae; see also GIBBS, HEGNAUER.]

WOODSON, R. E., JR., & R. W. SCHERY. Zingiberaceae, Cannaceae, Marantaceae. *In:* Fl. Panama. Part III. Fasc. 1. Ann. Missouri Bot. Gard. **32:** 57–105. 1945. [Severe criticism of Kränzlin's revision of *Canna*; *Canna glauca, C. flaccida, C. indica, C. edulis,* 76–78; *Maranta arundinacea,* 101; *Thalia geniculata,* 104.]

WUNDERLIN, R. P. Guide to the vascular plants of Central Florida. 472 pp. Tampa, Florida, & other cities. 1982. [*Musa paradisiaca* (persisting after cultivation and locally spreading vegetatively), *Alpinia Zerumbet* (rarely escaped, disturbed sites), *Hedychium coronarium, Canna* (3 spp.), *Thalia geniculata,* 143, 144.]

ZINGIBERACEAE Lindley, Key Struct. Phys. Syst. Bot. 69. 1835, nom. cons.

(GINGER FAMILY)

Aromatic, small to large herbs with short, distichous-scaly, thickened [or long, thin] rhizomes, these branching sympodially from axils of scale leaves near the bases of erect [or sometimes very short] stems, each branch potentially terminating in an unbranched leafy shoot [branched in some Costoideae] and/or an inflorescence. Hairs unicellular (Zingiberoideae). Plants with aromatic oil cells (Zingiberoideae). Leaves basal or cauline, sometimes petiolate, distichous [spirally arranged in Costoideae]; sheaths overlapping (in Zingiberoideae often forming a pseudostem surrounding or overtopping a thin true stem), open [or closed], adaxially ligulate at insertion of petiole; blade often asymmetric; stomata mostly tetracytic (paracytic to polycytic). Inflorescence(s) terminal [sometimes falsely appearing to be lateral], borne on a leafy shoot [or on a peduncle covered by distichous, bladeless sheaths arising from the rhizome], usually simple [sometimes branched or uniflorous], often with a condensed headlike or conelike appearance, the main axes bearing spirally arranged [or rarely distichous] primary bracts subtending variably modified [sometimes 1-flowered], condensed cincinni, these with variable higher-order bract(eole)s, sometimes with basal 2-keeled prophylls. Flowers perfect [rarely imperfect], highly diverse in appearance, usually lasting only 1 day, mostly zygomorphic. Sepals connate into a tube (sometimes not readily distinguishable as 3 units), the tube usually split along 1 side and lopsided. Petals fused basally with the androecium into a usually narrow tube, the dorsal lobe usually larger than the other lobes [and sometimes appendaged]. Androecium highly modified, variable in appearance, composed of 1 fertile stamen; a usually large, petaloid, often 2-lobed labellum (usually the largest organ of the flower); and sometimes 2 petaloid [to toothlike] lateral staminodes more or less free [or fused to labellum]. Anther with 2 locules [sometimes variably broadened or appendaged]; pollen grains 2-nucleate when shed, usually inaperturate (Zingiberoideae), spinuliferous to more or less psilate. Gynoecium usually with 2 variable "epigynous glands" (nectaries) jutting into the floral tube apically from the ovary (Zingiberoideae); ovary 3-locular with axile placentation [or 1-locular with parietal, basal, or free central placentation, rarely 2-locular]; ovules more or

less anatropous, usually numerous; style thin, usually passing through a channel in the filament and between the locules of the anther; stigmas diverse in form, usually ciliate, often sunken. Fruit capsular [or indehiscent, then fleshy or dry, sometimes opening by disintegration of the walls]. Seeds usually arillate, operculum well [to poorly] developed, endosperm development helobial, with perisperm and endosperm (sometimes with variable intrusions of chalazal tissue); embryo straight, cylindrical, or club shaped. Megagametophyte (embryo sac) of the Polygonum type (Zingiberoideae) [Adoxa type reported in *Costus*]; base chromosome numbers variable, including 9, 11, 12. (Including Costaceae Nakai, Jour. Jap. Bot. **17:** 203. 1941; Alpiniaceae Small, Man. Southeast. Fl. 360. 1933.) TYPE GENUS: *Zingiber* Boehmer, nom. cons.

A pantropical (to subtropical) herbaceous family, comprising over 1000 species in some 40–50 genera (over a third of these with very few species), typical of floors of lowland forests. Subfamily Zingiberoideae, encompassing by far the greater part of the family and subdivided into four tribes, is centered in tropical mainland Asia and the Malay Archipelago including Papuasia; only *Renealmia* L. f., nom. cons. (ca. 75 spp.), extends naturally to the New World. (It also occurs in Africa.) Subfamily Costoideae (Meisner) K. Schum. is made up of the pantropical *Costus* (80^{+} spp.), the small genera *Dimerocostus* Kuntze and *Monocostus* K. Schum. in tropical America, and *Tapeinochilos* Miq., nom. cons., which ranges from eastern Indonesia to Queensland. No extant species of Zingiberaceae is indigenous to the continental United States.

In Florida *Alpinia Zerumbet* (Pers.) B. L. Burtt & R. M. Sm. (*A. speciosa* (Wendl.) K. Schum.; *Languas speciosa* (Wendl.) J. K. Small), of tribe Alpinieae, persists after (or infrequently escapes from) cultivation, and *A. officinarum* Hance reportedly persists after cultivation (see Lakela & Craighead; Morton, 1976; Poppleton *et al.*; Small; Ward; Wunderlin; and acknowledgments), but neither appears to have become a component of the local flora. In Florida *Hedychium coronarium*, of the tribe Hedychieae, is more widespread outside of cultivation than the species of *Alpinia*.

Zingiberaceae are characterized vegetatively as mostly terrestrial, rhizomatous, sometimes large herbs with aromatic oils in specialized cells (Zingiberoideae) and with ligulate leaf sheaths. Diversity in overall form disguises a basic floral construction that helps to unify the family: the tubular calyx tends to split along one edge; the corolla and androecium form a tube, from which arise three petals, often two petallike to toothlike (or inconspicuous or absent) lateral staminodes, one fertile stamen bearing a complete anther, and a usually large labellum formed by the fusion of at least two staminodes. The thin style characteristically lies in a groove in the filament and passes between the locules of the anther. The arillate seeds contain straight embryos.

Polyploid and aneuploid changes are notable aspects of the evolutionary history of the Zingiberaceae. In fact, according to Sharma & Bhattacharyya, visible changes in chromosome complements have been sufficiently pervasive for different species typically to have different karyotypes. These authors, who studied both wild and cultivated Zingiberaceae, found that chromosomal heterogeneity is significant even within individuals. A second noteworthy cyto-

logical aspect of the family is that it should probably be counted along with the Juncaceae, Cyperaceae, and Musaceae(?) as one of the few families containing species that have chromosomes with diffuse centromeres (Grant).

A taxonomic history is available in Holttum's (1950) partial revision of the Zingiberaceae; historical notes and a compilation of important recent papers appear in Burtt (1972). In a paper rich in information on older literature, Burtt & Smith (1972a) concentrated on 47 "key species" in an attack on the snarled early history of the family. Because so much has been written about the Zingiberaceae, the present historical discussion is limited to selected recent changes and major problems, the most controversial of which may be the choice of rank for the group often called subfam. Costoideae.

Subfamily Costoideae is commonly raised to the rank of family by modern authors, particularly those concerned with systems of classification and interrelationships of families on a broad scale (Cronquist; Dahlgren; Takhtajan; Thorne; and Tomlinson, 1962, 1969). In contrast, others who have worked intensively on the taxonomy within the groups under consideration have relegated Costoideae to the subfamilial rank (Burtt & Smith, 1983; Holttum, 1950; Maas, 1972 and subsequent updates), and Hutchinson gave it only tribal status.

That differences separating Costoideae from other Zingiberaceae span a wide spectrum of characters helps to counterbalance the fact that many of the differences are based on small samplings of species. Costoideae stand apart vegetatively in having strongly developed main stems, spirally arranged leaves, closed leaf sheaths (also true of some Zingiberoideae—see Spearing) bearing ligules of a characteristic nature (Tran van Nam), and no aromatic oil cells. The flowers have nectaries confined within cavities (vs. rising into the floral tube), may differ in anatomical details (Rao *et al.*), and lack apparent lateral staminodes, which is also true of some Alpinieae, and which is possibly due to fusion with the labellum. Embryologically, Costoideae may be distinguishable by the nature of the nucellus, by having a tetrasporic (vs. monosporic) megagametophyte (Mauritzon) and an expanded cotyledon (vs. being haustorial—see Weisse, 1932), and by additional characters. Pollen of Costoideae is usually panto- or diaperturate (vs. mostly inaperturate) and has thin to thick exines (cf. *Hedychium, Canna*—see Erdtman; Maas, 1972; Punt). The two groups are further separated by differences in anatomy (Tomlinson, 1956, 1962, 1969), flavonoids (Williams & Harborne), and centers of distribution. Most, but not all, chromosome numbers in Costoideae are multiples of nine, but the broadly ranging numbers in Zingiberoideae also include multiples of nine. Raghavan & Venkatasubban's assertion that chromosomal morphology is another distinction was not borne out by Sharma & Bhattacharyya.

Beyond the evident need for confirmatory surveys, reluctance of some authorities to elevate Costoideae to the rank of family may rest partly upon the emphasis given technical and vegetative characters versus that given the fundamentally "zingiberaceous" flower structure that links the two groups. Flower structure is traditionally a weighty character for delineating families of Zingiberales.

Schumann (1904 and earlier) broke subfam. Zingiberoideae into three tribes

differing primarily in the number of locules in the ovary, the nature of the placenta, and the form of the lateral staminodes. Holttum (1950) transferred *Zingiber* from Schumann's Zingibereae (and consequently changed the name of this tribe to Alpinieae) to the Hedychieae, which should be renamed Zingibereae if this transfer is accepted. (Cytological support given by Mahanty for the transfer was dismissed as unsound by Burtt & Olatunji; better corroboration is provided by the plane of distichy of the leaves.) In 1972 Burtt & Olatunji placed *Zingiber* in a tribe of its own, thereby increasing the total of tribes to four: Alpinieae Meisner, Zingibereae (beware of disparate applications of this name), Hedychieae Duchartre, and Globbeae Meisner.[5] Dissatisfied with tribal delimitations, Burtt (1972; see also Burtt & Smith, 1972b; Smith, 1980a) discussed limitations on the taxonomic value of placentation and the nature of the lateral staminodes and agreed with Weisse (1933) that, although continued surveys are needed, the transverse plane of distichy on the aerial shoot in relation to the rhizome may distinguish Alpinieae from Hedychieae, in which the plane is parallel (as in Zingibereae *sensu* Burtt & Olatunji and those Globbeae examined by Weisse).

Zingiberopsis Hickey, a genus of three species of fossil leaves dating back to the Late Cretaceous and known from Alberta, North Dakota, Wyoming, and Colorado, was placed in the Zingiberaceae by Hickey & Peterson. Widespread in Eurasian sediments of Eocene to Pliocene age, zingiberaceous trilocular fruits and arillate seeds of *Spirematospermum Wetzleri* (Heer) Chandler resemble those of the modern Asian *Cenolophon oxymitrum* (K. Schum.) Holttum (Friedrich & Koch, 1970, 1972).

Chemical information on Zingiberaceae is scanty in relation to the size of the family. The summary that follows was condensed chiefly from surveys in Gibbs, Williams & Harborne, and Hegnauer. The aromatic oils of Zingiberoideae are rich in monoterpenoids (among them linalool, camphene, pinene, sabinene, borneol, camphor, cineole, and many others—the last three, according to Hegnauer, often the chief constituents of the oil). Sesquiterpenoids (including bisabolene, curcumenes, humulene, caryophyllene, zingiberene, turmerone, atlantones, zerumbone) are common and (hydrocarbons among them) sometimes predominate in the oil. Likewise widespread among aromatic plants, phenylpropane compounds are represented in zingiberaceous oils, sometimes as major components, by cinnamic acid and at least one derivative. Flavonoids are abundant, and Zingiberaceae (a small sample of Zingiberoideae) "form a chemically well defined group in which a variety of common (quercetin and kaempferol) and more unusual (myricetin, isorhamnetin and syringetin) flavonols occur in glycosidic combination with glucuronic acid, rhamnose or glucose" (Williams & Harborne, p. 226).

Mostly because of their aromatic oils, derivatives of Zingiberaceae have been used since ancient times as spices and condiments, in perfumes, and medicinally. Among the many products obtained from the family are ginger (prin-

[5]Tribal names used here differ from those in Burtt (1972) in the spelling of Alpinieae and in the changed authorship of Hedychieae to reflect its valid publication by Duchartre (Dict. Hist. Nat. **13**: 356. 1849.)

cipally rhizomes of *Zingiber officinale* Roscoe); turmeric (rhizomes of *Curcuma longa* L. (*C. domestica* Valeton), an ingredient of curry powders and the source of a yellow dye used like the more expensive saffron); melegueta pepper (seeds of *Aframomum Melegueta* (Roscoe) K. Schum.); cardamom (capsules and seeds of *Elettaria cardamomum* (L.) Maton and substitutes from other species); and galangal (*Alpinia officinarum, A. Galanga* (L.) Willd.). An "arrowroot" starch is extracted from rhizomes of *Curcuma angustifolia* Roxb. and other species. Some of the many genera grown as ornamentals under warm conditions are *Alpinia, Hedychium, Kaempferia* L., *Nicolaia* Horan. (*Phaeomeria* Lindley ex K. Schum.), and *Roscoea* James Sm. Species from a number of genera have been used as sources of fibers or pulp. (Among several works dealing with economic aspects of Zingiberaceae are Burtt, 1977a, 1977b, 1980; Ilyas; Morton, 1981; Perry; Purseglove; Rosengarten; and Schumann.)

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1. **Hedychium** J. G. Koenig in A. J. Retzius, Obs. Bot. **3:** 61 ("73"). 1783.

Upright, often large (*H. coronarium* to 3 m tall), [frequently epiphytic] herbs, the unbranched, leafy aerial stems borne on horizontal rhizomes and dying after flowering. Leaf blade inserted immediately above the sheathing base [or

on a short petiole], usually attenuate at both ends, sometimes bearing soft, pale, matted hairs abaxially. Inflorescences usually spicate [rarely branched], with large, crowded, spirally arranged [or reportedly sometimes whorled], imbricate bracts covering the axes, each bract usually subtending multiple flowers [or the bracts divergent from the then exposed axis, enfolding 1 or more flowers]. Flower bracteolate, fragrant, white and often with yellow toward the base of the labellum and the bases of the lateral staminodes [or colored differently, the colors then usually yellows to reds or sometimes purple]. Calyx tube short, split along 1 side [or entire], 3-lobed to apparently 1-lobed, usually glabrous with indument concentrated at the apex (*H. coronarium*). Corolla tube long and slender, projecting beyond [or shorter than] the subtending bract, much longer than [or infrequently about as long as] the calyx. Lateral staminodes 2, broad, petaloid and showy; labellum, the broadest and showiest component of the flower, abruptly [or gradually] narrowed at base, usually apically cleft, the depth of apical notch, width, and overall shape highly variable, more or less obcordate in *H. coronarium* [to Y-shaped, wedge-shaped, or elliptic]; filament about as long as the labellum, sometimes slightly shorter [to much longer]; pollen grains spherical, inaperturate or uniaperturate (in *H. coronarium* the aperture, when present, ulceroid and not clear in surface view, *fide* Saad & Ibrahim). Ovary 3-locular, with many ovules per locule, glabrous to sericeous, the style filiform, lying in a groove in the corolla tube and filament, and protruding apically beyond the anther. Capsule loculicidal, 3-locular (fruiting specimens not seen from the United States). Seeds variably shaped, with initially red (becoming yellowish) arils, these lacerate on mature seeds. Base chromosome number mostly 17. TYPE SPECIES: *H. coronarium* J. G. Koenig.[6] (Name from Greek, *hedys*, sweet, and *chion*, snow.)

A genus of approximately 50 to 60 species, about a third of them described since Schumann's (1904) revision and many unclearly delimited, in two subgenera, HEDYCHIUM and EUOSMIANTHUS K. Schum.[7] The largely Himalayan center of distribution encompasses northeastern India, Bangladesh, the upper Ganges River, and Nepal. Continuing to the south and east with a diminished number of species, the probable natural range of *Hedychium*, outlined by southern China, Vietnam, the Philippines, Java, and Sulawesi, crosses Wallace's line but does not reach New Guinea or Australia. At the western extreme,

[6]Burtt & Smith (1972a, p. 190) have argued against rejection of this and others of Koenig's specific names due to publication in a work in which Linnaean binomials were not consistently used.

[7]Wallich (1853) and Horaninow (1862) each recognized four subgroups of unspecified rank, two of which remain of interest: "*Gandasulium* Horan." and "*Macrostemium* Horan.," adopted by Baker (1892) at the rank of section and distinguished by the relative lengths of the stamen and labellum. Later, Schumann (1904), employing characters of the inflorescence and its bracts, divided the genus into "subgen. *Gandasulium* Horan." and subg. *Euosmianthus* K. Schum. Lourteig (1972) changed the name of the former to subg. *Hedychium*, since it includes the type species of the genus, and adopted for the latter "subgenus *Macrostemium* Horan. (sensu *Euosmianthus* Schum.)," with *H. Gardnerianum* Wallich ex Roscoe as lectotype. Although earlier than *Euosmianthus*, *Macrostemium* was published without designation of rank and thus, according to the ICBN, 1978, lacks nomenclatural priority at the rank of subgenus. It seems reasonable, nevertheless, to maintain *H. Gardnerianum* as lectotype for subg. *Euosmianthus* K. Schum.

Hedychium peregrinum N. E. Br. is endemic to Madagascar. The natural distribution of *H. coccineum* Buch.-Ham. ex James Sm. doubtfully includes Sri Lanka (Burtt & Smith, 1983). Species of this widely cultivated genus are scattered in other regions largely, if not completely, as a result of human activity. *Hedychium coronarium* grows extensively outside of cultivation in warm regions worldwide. Habitats of species of *Hedychium* range from tropical to temperate, at altitudes approaching 3000 m, in usually (but not always) open, typically wet places: often shores, moist slopes, and edges of forests. Several species are epiphytic or facultatively so.

Subgenus HEDYCHIUM (subg. *Gandasulium* (Horan.) K. Schum.) (inflorescence compact, usually broadly ellipsoid or ovate in outline, with wide, imbricate bracts covering the rachis) is represented in the southeastern United States by *H. coronarium*, ginger-lily, butterfly-lily, garland flower, which has escaped cultivation into various wet habitats in Florida (and according to Small, but not substantiated in recent checklists, in eastern Georgia and southeastern Louisiana). Although obscured by cultivation, the natural range of *H. coronarium* probably lies within the generic center of distribution described above. In that region *H. coronarium* is fertile (see, for example, Roxburgh, Mukherjee), although in some or all of the regions into which it has been introduced, production of fruit appears to be rare. Harling thought deficiency of pollinators to be a more likely explanation for low fertility of this species in Ecuador than incompatibility between members of the probably highly clonal population there. Self-incompatibility, however, has been reported in *Hedychium* (Holttum, 1950), and the plant illustrated in FIGURE 1 failed to set fruit with its own pollen. These reproductive limitations notwithstanding, *H. coronarium* can be an aggressive invader aided by strong rhizomatous growth and possibly distributed by fragmentation and flotation of rhizomes. It forms dense clumps or extensive colonies, in tropical America covering large areas and reportedly sometimes having a deceptively indigenous appearance (Beadle, Standley & Steyermark).

The name "*Hedychium coronarium*" is applied to various portions of a problematic complex that also involves the names *H. maximum* Roscoe, *H. flavum* Roxb. (non Roscoe), *H. flavescens, H. chrysoleucum* Hooker, *H. urophyllum* Lodd., *H. Elwesii* Baker, and *H. subditum* Turrill (*H. flavum* Roscoe). Baker treated most of these as varieties of *H. coronarium* separated from each other primarily by the coloration of the flowers. Emphasizing this character and the shape of the labellum, Schumann (1904) elevated most to specific rank, as did Turrill in a thorough, illustrated discussion of the matter. In Turrill's paper an expanded set of vegetative and reproductive characters augments the persistently important floral coloration. Studying living plants, Naik & Panigrahi uncovered intergradation in the colors of flowers among the species; they preferred using the structure of the inflorescence and the form of the labellum for taxonomic purposes and reassembled *H. coronarium* in its broader sense. Orchard, Lourteig, and Burtt & Smith (1983) have separated *H. flavescens* from *H. coronarium* at the specific level. If judged from the works cited above, *H. coronarium* sensu stricto is characterized by having the flower purely white or tinged with yellow or green, the calyx glabrous or nearly so and proportionately

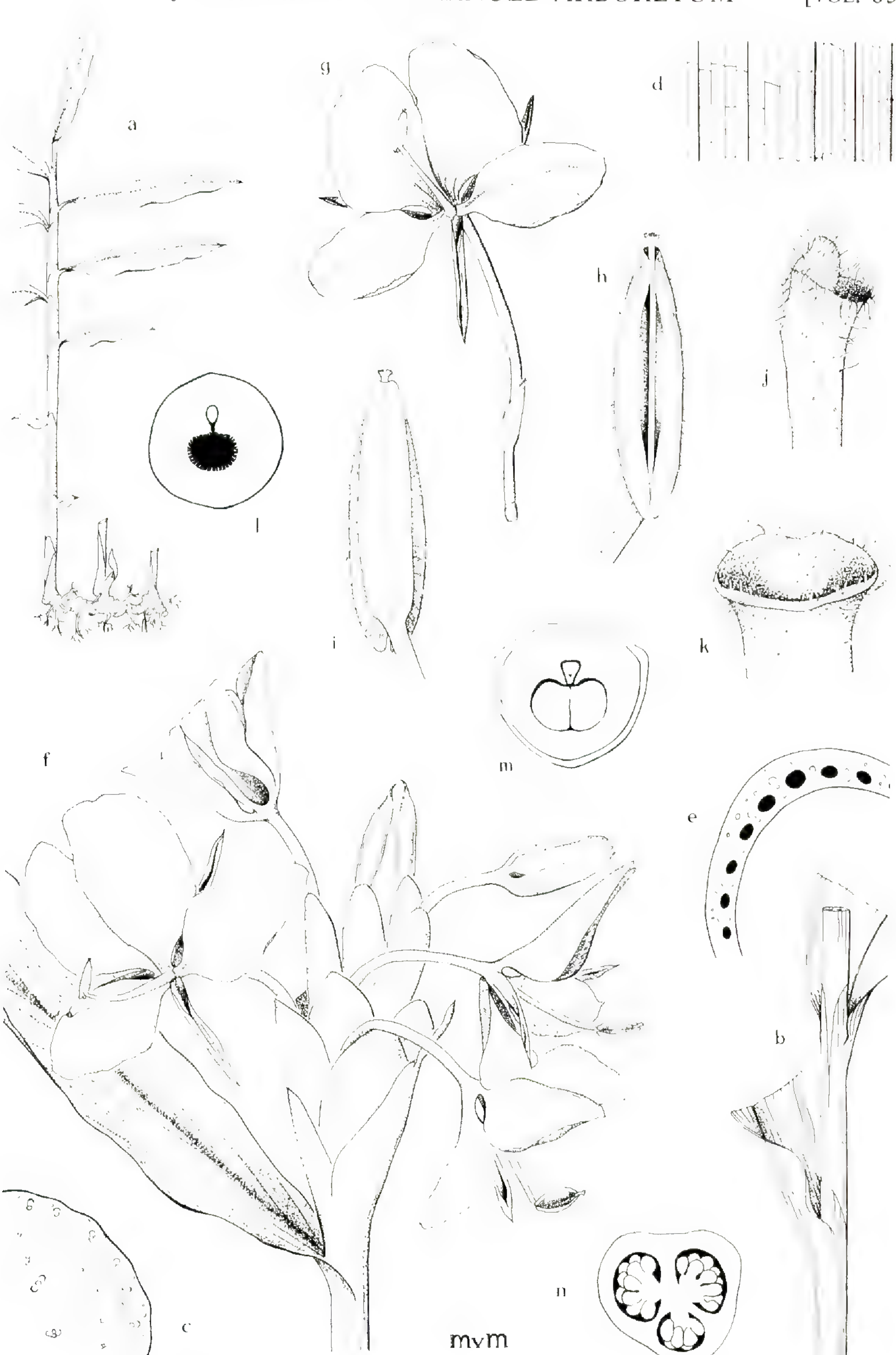

FIGURE 1. **Hedychium.** a–n, *H. coronarium:* a, unbranched stem rising from horizontal rhizome, × 1/12; b, portion of stem showing ligulate leaf bases, × 1/2; c, cross section of stem, × 6; d, detail of leaf showing venation, × 6; e, cross section of leaf sheath, × 6; f, inflorescence, × 1/2; g, flower, showing split, 1-lobed calyx, narrow petals with incurled margins, 2 broad lateral staminodes, labellum with bifid apex, and single sta-

short, the labellum about as wide as long, and the white staminal filament either about as long as or shorter than the labellum. The complex as a whole is recognized by having each bract with multiple mostly white to yellow flowers, each with a large labellum and usually broad lateral staminodes.

As a genus, hedychiums are robust rhizomatous herbs with unbranched aerial stems bearing terminal, usually spicate, many-flowered inflorescences. The fragrant flowers, usually a few per bract, tend to have lopsided calyces usually split along one side; each flower has a longish, narrowly cylindrical corolla tube with none (vs. one in *Odontychium* K. Schum.) of the lobes appendiculate; two strongly developed (vs. inconspicuous in *Alpinia*), petallike lateral staminodes; a protruding (vs. very short in *Brachychilum* (R. Br. ex Wall.) Petersen), usually bilobed, or emarginate labellum with an otherwise entire (vs. denticulate in *Odontychium*) margin; and a long, exserted stamen. As an example illustrating that "a number of genera [in Zingiberoideae] may be distinguished by their leaf flavonoid profiles," Williams & Harborne (p. 224) pointed out that myricetin glycosides are the predominant flavonoids in *Hedychium* (9 species studied).

Smith (1980a) found the new genus *Stadiochilus* R. M. Sm. to resemble *Hedychium* in having the corolla tube grooved to accommodate the style (known also in *Brachychilum* and *Zingiber*), in the form of the corolla lobes, and in having a long filament. Smith (p. 14) stated that "if a pair of petaloid lateral staminodes were added to *Stadiochilus* we should have a perfectly good *Hedychium* rendered slightly anomalous by the upright, rather pendulous labellum."

Most chromosome counts in *Hedychium* have yielded the somatic number 34, although the genus appears to be prone to polyploidy and aneuploidy, with numbers varying even within species (see especially Mukherjee). The following somatic numbers have been reported in species of *Hedychium*: 18 (*H. coronarium*, see Hsu), 24 (reported once in *H. thyrsiforme* Ham., but contradicted by further study—see Mahanty), 26, 36, 50, 51, 52, 54, 66, and 68. Most of these numbers up to 66 have been reported in *H. coronarium* sensu lato, as well as in other species. Raghavan & Venkatasubban observed general similarity in the size and morphology of chromosomes among the six(?) species of *Hedychium* that they studied. Similarly, although the chromosomal morphology was not identical in any two taxa, Sharma & Bhattacharyya noted "a gross resemblance" among 10 species and varieties of *Hedychium*. Those two authors, in good agreement with Mukherjee, found the chromosomes of *He-*

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men, × ½; h, adaxial side of anther (note thin style passing between the 2 locules, the stigma protruding apically), × 3; i, abaxial view of anther, × 3; j, lateral view of stigma, × 15; k, adaxial view of stigma, × 15; l, diagrammatic cross section of corolla tube above calyx, the lumen in black, the style in groove above lumen unshaded, × 6; m, diagrammatic cross section of flower slightly above ovary, showing calyx (outer unshaded layer not adnate to corolla tube), corolla tube (unshaded), 2 epigynous nectar glands, and style (in groove in corolla tube), × 6; n, diagrammatic cross section of ovary, showing locules and axile placentae, × 6.

dychium generally to be short, varying gradually in length within each complement. The different potential species of *Hedychium* studied by Sharma & Bhattacharyya had chromosomes with the primary constrictions nearly submedian to median and varied in the numbers of pairs bearing secondary constrictions. Mukherjee and Sharma & Bhattacharyya reported meiosis in *H. coronarium* to be mostly normal or nearly so; Mukherjee recorded 96 percent pollen fertility in material from northeastern India. According to Holttum (1950), hybrids are easily produced in *Hedychium*.

The three main layers of the walls of pollen grains in *Hedychium* resemble those of the more thoroughly studied *Canna* and certain other genera. In *Hedychium coronarium* a grainy, thin, acetolysis-resistant, presumably exinous layer overlies a thick, acetolysis-degradable, almost certainly intinous layer with a radially patterned infrastructure. The third, innermost layer is hygroscopic and lacks a radial pattern (Erdtman & Praglowski). Although generalizations would be premature and substantial variations have turned up, there are indications that pollen roughly as described above may be widespread among Zingiberales (see Saad & Ibrahim; Erdtman, 1963; Hesse & Waha, under *Canna*; Kress *et al.*; Kress & Stone, under *Canna*).

Meager data point to sphingids as the predominant pollinators of *Hedychium coronarium* and probably most other species of the genus. Pollen may sometimes be transferred on the wings of butterflies (Müller).

Accessory embryos were observed to arise from synergids but not to develop beyond early stages in *H. acuminatum* Roscoe (Sachar & Arora).

Hedychium coronarium, *H. coccineum*, *H. Gardnerianum* Roscoe, *H. spicatum* Buch.-Ham. ex James Sm. (see Winters & Corbett) and several other species are cultivated, mostly under warm conditions. The fragrant, showy flowers of *H. coronarium* are valued for making Hawaian leis (see Neal). Volatile oils from flowers and rhizomes of this and possibly other species are useful in perfumery. Rhizomes of *H. spicatum*, sometimes sold as the drug "kapur(a) kachari" and sometimes in a fragrant powder, abir, lend their scent to tobacco, incense, soaps, face powders, hair oils, and fabrics, and they are thought to repel insects. Medicinal uses of derivatives of *H. spicatum* and other hedychiums are available in Chaturvedi & Sharma, Cooke, Dixit & Varma, Perry, Pineda-Ocampo *et al.*, Sastri, B. D. Sharma (1974, 1975), and the papers by S. C. Sharma *et al.* *Hedychium coronarium* has attracted attention as a rapidly growing source of pulp for paper. This rhizomatous species sometimes becomes a weedy pest in places where sugar cane is grown (Beadle).

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CANNACEAE A. L. Jussieu, Gen. Pl. 62. 1789, "Cannae," nom. cons.

(CANNA FAMILY)

Large, usually rhizomatous herbs with unbranched aerial stems. Leaves large, with open, eligulate sheaths. Flower asymmetric, with a staminodial lip (labellum) and a variable number of additional petallike staminodes [or none], 1 fertile, partly petaloid stamen, and 1 more or less flattened, colorful style rising from a 3-locular ovary with septal nectaries. TYPE GENUS: *Canna* L.

1. **Canna** Linnaeus, Sp. Pl. **1:** 1. 1753; Gen. Pl. ed. 5. 1. 1754.

Plants often 1 to several meters tall, often glaucous, mostly glabrous (sometimes with an ephemeral, woolly indument on leaves and stem [or inflorescences]). Rhizomes branching sympodially, sometimes thickened, these and aerial stems with mucilage canals or cavities. Leaves with the blades often asymmetric, the sheath clasping the stem to the insertion of the blade or partly free; stomata predominantly paracytic. Inflorescences terminal on leafy shoots, spicate or branched, each branch with a 2-keeled prophyll. Flowers showy, in homodromous cincinni of 2 flowers (1 flower of the pair typically not developing, rarely with 3 flowers), each flower or pair subtended by a bract and sometimes with scalelike bracteoles, erect [to pendulous], colors mostly yellows and reds. Sepals 3, free, persistent, lanceolate to elliptic. Petals 3, usually unequal, usually basally connate and adnate to the androecium and style to form a tube, upright or reflexed, deciduous. One stamen fertile and partly petaloid, enfolding the style in the bud, with a marginal anther, this sometimes appearing superficially to be 2-locular (but generally interpreted as a 1-locular half-anther); the other androecial members sterile, one of these curled [or straight] forming the labellum, the remaining 3 or 2 [or none in subg. *Distemon*] mostly large, erect, broadened, and petallike (flowers rarely with a fifth sterile staminode); pollen deposited onto the side of the style in the bud, the pollen grains mostly spherical, usually with small spinules, inaperturate (sometimes with 1 or 2 pores *fide* Nair, 1962). Ovary covered with conspicuous, sap-bearing protuberances, each of the 3 locules with numerous anatropous ovules on an

FIGURE 2. **Canna.** a–q, *C. flaccida:* a, young aerial shoot coming from underground rhizome, × ¼; b, blade and portion of petiole of nearly mature leaf, × ¼; c, detail of upper part of sheathing petiole—ligule not present, × ¾; d, inflorescence with open, nocturnal flower and flower bud, both in side view—on open flower note bractlike sepals

axile placenta; style opposite the fertile stamen; stigmatic surface terminal and decurrent along an edge of the style. Capsule globose to oblong-ellipsoid, tuberculate-bristly, loculicidally dehiscent or the seeds released by breakdown of the pericarp. Seed globose or nearly so, dark colored, hard, opening by a slit, with an arillike tangle of hairs arising from the funiculus, these hairs remaining in the fruit; with abundant nutritive tissue ("chalazosperm") derived from the chalazal region; endosperm initially nuclear, reduced to a thin layer in the mature seed. Embryo linear, straight, extending into a cavity at the end of the seed. Radicle and plumule developing apart from the remnant of the seed, connected to it by a cotyledonary appendage. Megagametophyte (embryo sac) essentially of the Polygonum type. Base chromosome number 9. LECTOTYPE SPECIES: *C. indica* L.; see N. L. Britton, Fl. Bermuda, 86. 1918. (Name from Greek *kanna,* cane.)

A distinctive monogeneric family with a problem-free circumscription, in contrast with its internal taxonomic and nomenclatural disarray. The usually quoted estimate of about 50 species in *Canna* was approximately halved in the revision by Segeren & Maas, and according to Jiménez (citing personal communication), Maas has since compressed his estimate to only seven species. The genus is centered in the American tropics and subtropics, including the West Indies; species occupying scattered warm areas in the Old World were probably introduced by humans, although agreement on this point is not unanimous.

Cannas are characterized by an asymmetric, showy flower with a staminodial labellum, two or three large, relatively unspecialized, petaloid, sterile staminodes (in ours), and one partially petaloid fertile stamen. The inferior ovary and capsule are tuberculate, the capsule containing several dark-colored, hard, nearly spherical seeds with stomata on the seed coats and a tangle of emergences on the funiculus. The leaves lack ligules and pulvini. Mucilage canals pass through the rhizomes and unbranched aerial stems.

The four genera of Cannaceae recognized by Horaninow were reduced to sections and subgenera of *Canna* by Petersen (1888) and Baker (1893), respectively. In the only revision of the entire genus written during the twentieth century, Kränzlin retained subg. DISTEMON (Bouché) Baker and, subsuming

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at base, reflexed petals, and 5 dissimilar, petaloid staminodes (labellum to lower left, 2 small sterile staminodes to upper right under the letter "d"), × ½; e, frontal view of open flower, labellum to lower right, fertile half-anther and tip of stigma visible in center of flower, × ½; f, detail of flower to show reflexed petals, × ½; g, expanded staminode, × ½; h, fertile stamen with half-anther attached to left margin, × ½; i, detail of half-anther after dehiscence, × 3; j, vertical section near center of flower to show petals, staminodes, and style adnate to floral tube, × 1; k, tip of style showing stigmatic line around apex, × 2; l, diagrammatic cross section of inferior trilocular ovary, 3 septal nectaries visible as black slits near center, the wall finely tuberculate, the ovules anatropous, axile, × 5; m, mature capsule crowned by persistent sepals, × ½; n, mature seed, × 3; o, detail of seed coat showing finely pitted surface (with stomata—not visible), × 25; p, seed in diagrammatic section (cut along line indicated by arrow in "n"), "chalazosperm" evenly stippled, × 3; q, seedling still attached to seed, × ½.

Baker's other subgenera in subg. (Eu-)CANNA, divided the latter into sects. BIALATAE and TRIALATAE. Section TRIALATAE (which should be called sect. CANNA) comprised four subsections. Winkler's infrageneric classification was essentially the same, except that the subsections were designated series. In a revision of the species in northern South America, Segeren & Maas thought it "very doubtful" that sections BIALATAE and TRIALATAE should be maintained and did not keep them in their formal treatment, which is the course accepted in the present paper.

Subgenus CANNA (staminodes two or three, in addition to the labellum; labellum reflexed) is represented in the southeastern United States chiefly by *Canna flaccida* Salisb., $2n = 18$, which is probably the only indigenous species. Sometimes called "golden canna," "yellow canna," or "bandana of the everglades," it occurs on the Coastal Plain from South Carolina to Texas, and in the West Indies, Central America, and northwestern South America. Flowers of this striking species have reflexed petals and very showy, broad, soft, yellow staminodes with undulate margins; the bases of the leaves are gradually tapered. A similar species with a wide range in warm regions south of the United States, *C. glauca* L., $2n = 18$, has been reported from Louisiana and Texas (see Thieret; *Godfrey & Tryon 274* [GH] from South Carolina is probably also referable to this species). *Canna glauca* (*C. angustifolia* L., *C. stricta* Bouché, both synonyms from Segeren & Maas) differs from *C. flaccida* most saliently in its erect petals and narrower staminodes. (Whether or not the staminodes of *C. glauca* are mottled is a point of disagreement.) *Canna indica*, indian-shot (with an ample synonymy), $2n = 18, 27$ (also probably 36; plus other dubious numbers reported), has escaped cultivation sporadically in the Southeast, as well as in much of tropical Asia, Africa, and elsewhere. This species was cultivated in Europe as early as the sixteenth century. Its capsules and predominantly red flowers marked with (or sometimes entirely?) yellow are smaller than those of the preceding species (e.g., the widths and lengths of the staminodes are about 1–1.5 × 4–6 cm vs. 1.5–2 × 8–10 cm in *C. glauca* and 8–9 × 9–11 cm in *C. flaccida*; measurements from Segeren & Maas). *Canna indica* sometimes produces fertile hybrids with *C. glauca* despite some meiotic irregularities and diminished fertility. *Canna edulis* Ker-Gawl., $2n = 18, 27$, often cultivated for its edible rhizome, appears in Ward's checklist of plants native or naturalized in Florida and as a synonym of *C. indica* in Segeren & Maas.

Described by Kränzlin as "ein uferloses Meer," the cultivated cannas are an assortment of probably over 1000 horticultural varieties. Most of these fall into two main groups, both of which persist following cultivation or escape in the Southeast: *Canna* × *generalis* Bailey does so sporadically in several states, and *C.* × *orchiodes* Bailey was reported as growing apart from cultivation in North Carolina by Crutchfield. Flowers of these two diverse, intergrading hybrid lines are large (reaching 20 cm in diameter in *C.* × *orchiodes*) and display a rich array of colors, mostly reddish and yellowish hues, sometimes pastels or white, with the staminodes often spotted, streaked, and bordered. Foliage and stems are bronzed in some. Because *C. flaccida* is a genetically influential ancestor of *C.* × *orchiodes*, confusion between these two is especially likely. *Canna flaccida* has a longer floral tube (over 5 cm vs. ca. 2.5–5 cm in *C.* ×

orchiodes and less than ca. 1.5 cm in *C.* × *generalis*) and a longer capsule (4–6 cm vs. shorter and sterile in *C.* × *orchiodes*). Both *C.* × *orchiodes* and *C. flaccida* differ from *C.* × *generalis* and the other species in having petals reflexed or becoming so and flowers that are generally more delicate and flowing. (For further comparison of the large-flowered cannas, see Bailey, 1923; Crutchfield; and Mukherjee & Khoshoo, 1970d.)

Much literature on *Canna* revolves around elucidating the ancestry and cytology of *C.* × *generalis* and *C.* × *orchiodes* and morphological changes that have taken place in the course of their development since the mid-1800's. The history of the cultivars is clouded by loose application of names in early records. From the multifaceted investigations along these lines by Mukherjee and Khoshoo, *Canna glauca, C. indica, C. iridiflora* Ruiz & Pavon, and *C. Warszewiczii* A. Dietr. stand out as the most likely principal progenitors of the multiple lineages known as *C.* × *generalis*. Selected additional (but not entirely congruous) references useful in this connection are Anonymous (1898), Bailey (1923), and Donahue.

Like their four supposed ancestors, most cultivars of *Canna* × *generalis* are diploids with normal or nearly normal meiosis. A small proportion are meiotically irregular interchange heterozygotes; others are sterile triploids that tend to form trivalents at metaphase I.

During the 1890's, plants of *Canna* × *generalis*, in this case "Crozy cannas," were crossed with *C. flaccida* to yield *C.* × *orchiodes*. That the genome of *C. flaccida* is strongly differentiated from those of the putative ancestors of *C.* × *generalis* is suggested by the complete sterility of *C.* × *orchiodes*, which has highly irregular meiosis in its diploid cultivars and forms few, loose trivalents in the triploids. On the other hand, Kränzlin mentioned fertile hybrids between *C. flaccida* and *C. Warszewiczii*. (The accuracy of this report depends upon the accuracy of Kränzlin's opinion that a plant breeder misapplied the name *C.* "*nepalensis*" to *C. flaccida*.) Baker (1894) described *C. flaccida* × *iridiflora* as the origin of (fertile?) fine garden forms.

If one considers the genetic intercompatibility among (and not limited to) the probable ancestors of *Canna* × *generalis*, confusion in defining species of *Canna* is hardly surprising. A related confounding factor is that cannas have long been transported about the world by humans (undoubtedly with operation of the founder principle, release of segregating hybrid progeny into new habitats, vegetative propagation of new forms, and artificial selection). The pantropical complex centered around *C. indica* is a troublesome example, involving several possible species. A second puzzling example is *C. flaccida*, which differs only slightly from *C. Reevesii* described by Lindley from specimens grown from seeds sent to him from China.

A further source of taxonomic confusion in *Canna* is a likely overemphasis of certain characters. For instance, in a series of papers, Honing analyzed the genetics of the coloration of flowers and vegetative parts in *C. glauca, C. indica*, and other possible species. In 1939 (VI) he explicitly rejected Kränzlin's classification, concluded that the most obvious differences distinguishing *C. indica* and certain other "bialatae" depend on only a few Mendelian factors, and proposed placing five names (including *C. indica*, excluding *C. glauca*) in syn-

onymy. (Honing's studies were summarized by Khoshoo & Mukherjee (1970b), who suggested that members of nearly the same collection of species, including both *C. glauca* and *C. indica,* may be differentiated at an ecospecific level.) Red color in the flowers is a monogenic dominant trait influenced in expression by at least 22 other genes and linked to a set with recessive lethal alleles. The presence of two vs. three staminodes in addition to the labellum has repeatedly emerged (e.g., Baker, 1894; Costerus, 1916a; Jiménez; Kirchoff, 1983b; Segeren & Maas) as a character of questionable taxonomic value, varying within a species and even on a single plant, yet this character alone distinguishes Kränzlin's sections "Bialatae" and "Trialatae."

Species of *Canna* are predominantly diploids with $2n = 18$. Triploidy (which appears to have arisen repeatedly in artificially selected cultivars) and infrequent tetraploidy have been detected only in species for which diploid counts are also reported. (Compilations of chromosome numbers are available in Segeren & Maas; Mahanty; Khoshoo & Mukherjee, 1970a; Sharma; and Satô). Satô described and illustrated chromosomal morphology for *Canna edulis, C. indica,* and *C. glauca,* all $2n = 18$, which differ from each other in distributions of lengths of chromosomes, positions of centromeres, and locations of satellites and secondary constrictions. Mahanty concluded from a study of six species that species of *Canna* form a very homogeneous group.

As in Marantaceae, the pollen in Cannaceae is deposited on the style while in the bud, either directly onto or near the stigma. It is widely assumed, although hardly tested, that self-fertilization plays an important role in the breeding system. Mukherjee & Khoshoo (1970b) (see also Darwin) found the few "elemental" species that they studied, cultivated outside of their natural ranges, to be predominantly autogamous, whereas displacement of the anther and stigma necessitated a shift to outbreeding in the cultivated hybrids. (Garden cannas are usually propagated vegetatively.)

The fragrant flowers of *Canna flaccida* open about dusk for a single night throughout the year in South Florida. Swamps, marshes, shores, and pine savannas are the habitats of this species; in the United States *C. glauca* and *C. indica* likewise occupy wet places. This is at least sometimes true of hybrid cultivars growing outside of cultivation.

In much of the American tropics and subtropics, including the southeastern United States, *Canna* is larval host to a skipper butterfly, *Calpodes ethlius* (Cramer), which at times is severely destructive to the plants (see Clark & Clark, Cockerell, Evans, Young) and which is a pest on the related *Maranta arundinacea* grown commercially in the West Indies (Purseglove). The larvae, which build tentlike structures protected by rolled or folded leaves, are parasitized by possibly two genera of wasps.

As determined for *Canna* × *generalis* and *C. indica,* the thick wall of the pollen grain has three main layers. Much reduced, the exine, which takes the form of scattered spinules and may also extend around the grain as a thin skin (Hesse & Waha), rests on a thick, bilayered intine. The outer intinous layer, the "exintine" (Kress & Stone), is honeycombed with radial channels and overlies the unchanneled "endintine." Comparable in structure to germinal pores of more typical pollen grains, the "omniaperturate" grains of *Canna*

appear to have their entire surface suitable for hydration, other interactions with the stigma, and emergence of the pollen tube. The channels in the intine possibly function as reservoirs of compounds connected with incompatibility mechanisms or otherwise with germination of the pollen (Hesse & Waha). For details on the structure of the pollen, see Kress & Stone, Rowley & Skvarla (1974, 1975), Scheer & Franke, Skvarla & Kelly, and Skvarla & Rowley. (Also see discussion of *Hedychium* in the present paper.)

Useful not only as ornamentals, some species of *Canna* have starchy rhizomes, for which especially *C. edulis* is used as a source of food for livestock and humans. Possibly first domesticated in northern South America (Gade), this species is cultivated in warm regions around the world, sometimes on a commercial scale. The product from Australia is called "Queensland arrowroot." A current project of the New York Botanical Garden Institute of Economic Botany is the development of a clone of *Canna* with the largest starch grains known from any plant. The hard, more or less spherical, dark-colored seeds have been employed in sundry easily imaginable ways from ammunition to rosary beads, and they have also been used as an ingredient in a substitute for coffee. One example sufficiently underlines their renowned durability: a seed about 600 years old taken from within a rattle recovered from an Argentinian tomb grew into a flowering individual of *Canna compacta* Roscoe (Lerman & Cigliano). Burning the plants is said to produce an insecticidal smoke. Extracts from *C. indica* and other species have molluscicidal activity of interest in the control of schistosomes (Mahran *et al.*). Additional uses of cannas, especially extensive medicinal applications, are listed in Hegnauer, Kränzlin, Morton (1981), and Perry.

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MARANTACEAE Petersen in Engler & Prantl, Nat. Pflanzenfam. II. **6**: 33. 1888, nom. cons.

(ARROWROOT FAMILY)

Erect [or scrambling or climbing] small to large herbs of diverse habit. Rhizomes branching sympodially, usually with short internodes. Plants glabrous or with usually unicellular hairs, each surrounded at the base by a cluster of inflated epidermal cells. Branches variably developed, sometimes clustered at or above the ground, often widely divergent, each branch bearing (in the following order) a basal, 2-keeled prophyll above a short internode, usually a bladeless sheath (interphyll) above a second short internode, a series of petiolate leaves, and a terminal inflorescence often overtopped by axillary growth [inflorescences sometimes arising directly from the rhizome]. Leaves typically distichous, basal or cauline, with open, often auriculate [rarely ligulate] sheaths, and often asymmetric [often variegated] blades, those of leaves on a shoot either homotropous (i.e., the broader halves all on the same side—right or left—of the midrib) [or antitropous, the broader halves on alternating sides]; petiole with a usually pubescent pulvinus at the insertion of the blade; stomata mostly paracytic. Inflorescences highly variable, [completely or] partly tightly condensed to diffusely branched, bracteate; bracts frequently large and colorful, mostly sheathing. Flowers asymmetric, usually in mirror-image pairs, each pair or group of pairs subtended by a bract and a basal prophyll, [with or] without bracteoles. Sepals free. Petals usually unequal and usually connate basally and adnate to the androecium and gynoecium to form a tube. Outer androecial cycle represented by [0 or] 1 or 2 antesepalous, petallike staminodes; the 3 members of the inner cycle all different: the "cucullate staminode"[8] forming a

[8]A disorderly profusion of names has been applied to the 2 inner sterile staminodes, both of which are hoodlike. Those adopted in the present paper are translated from extensive use in German and have been used in English by other authors. The cucullate staminode (FIGURE 3, g) is also known as the hooded staminode, Kappenblatt, Kapuzenblatt, or style-holding staminode. The callose staminode (FIGURE 3, h) has also been called the callosed or callused staminode, Schwielenblatt, and labellum. Particularly misleading, the last term is used for structures in Cannaceae and Zingiberaceae that are uniquely homologous within each family.

sterile pouch concave toward the axis of the flower and enclosing the style, with 1 or 2 appendages inserted on the edge away from the fertile stamen and arching over the concavity; the "callose staminode" bent into a hood, concave toward the axis of the flower (facing the concave side of the cucullate staminode), usually with a thickening protruding inward from the face of the side nearer the fertile stamen [or with a second thickening on the other side]; the fertile stamen usually borne on the side of the flower adjacent to the other flower of the pair, with a unilocular half-anther inserted laterally on [and sometimes adnate to] a petaloid appendage [this sometimes short and inconspicuous]. Gynoecium with 1 [or 3] locules developing and [0 or] 1 anacampylotropous fertile ovule per developing locule, this nearly basal on an axile placenta; nectaries septal; style curled inward upon release from the cucullate staminode, with a specialized pad basal to the stigma for deposition of pollen in the bud; stigma in a depression between 3 variably developed flaps. Fruit indehiscent or dehiscent into 3 valves, dry [or fleshy]. Seeds variable in shape, basally arillate [or not, especially in indehiscent fruits], hard, operculate; endosperm formation nuclear, endosperm much reduced or lacking in mature seed, perisperm abundant and penetrated by a curved or straight (sometimes basally forked) canal originating as a vascularized chalazal intrusion into the progressively curving nucellus; embryo U-shaped. Megagametophyte (embryo sac) fundamentally of the Polygonum type, antipodal cells sometimes undergoing secondary divisions. Chromosome numbers highly variable, the base numbers including 4, 6, 9, 11–13. TYPE GENUS: *Maranta* L.

A sharply defined family of 25 to 30 genera and probably more than 400 species (usually sorted into two tribes) typical of understory vegetation in wet regions pantropically, but sometimes reaching subtropical or infrequently warm-temperate areas. The greatest concentration of species is in the South American tropics, with lesser centers of distribution in tropical West Africa and tropical Asia. Especially widespread, the genus *Thalia* L. occurs throughout much of Africa, where it may or may not be indigenous, and from southern South America to the southeastern United States. (The family is also represented in Florida by *Maranta arundinacea*, an infrequent escape from cultivation.) Outstanding among the genera, which only exceptionally contain more than 20 species, *Calathea* G. F. W. Meyer probably encompasses considerably more than 130. This genus and *Thymocarpus* Nicolson, Steyerm., & Sivadasan are the only representatives of the tribe Phrynieae Petersen (ovary with three fertile locules and usually three fertile ovules) in the New World. The tribe Maranteae (ovary with one fertile locule and ovule) is restricted to the New World, except for *Thalia*, as mentioned above.

Marantaceae are unified as a family by their open, usually eligulate leaf sheaths and a pulvinus (or "callus") at the insertion of the blade. Tomlinson (1961) pointed out that the strongly developed aerial branching system sets the family apart from other Zingiberales (but the presence of a prophyll followed by one or more incomplete leaves is insufficient to distinguish Marantaceae).

The asymmetric flowers, usually borne in homodromous pairs, have a unique explosive pollination mechanism (described below), one or two showy outer staminodes, two hoodlike inner staminodes positioned face to face (one with one or two lateral appendages, the other usually with a thickening protruding from the surface), a half-anther connected to a petaloid appendage (also true of Cannaceae), and a uni- or trilocular ovary with one nearly basal ovule per locule. The abundant nutritive tissue in the usually arillate seed is penetrated by one or two canals. The embryo is curved.

While there has been little contention about the delimitation of the Marantaceae as a family, the definition and nomenclature of taxa within it have a troubled history. Although fundamental to the studies that followed, Koernicke's monographs (1859, 1862) bear little resemblance in detail to relatively recent treatments. Eichler provided detailed morphological analyses essential for comparing plants as complex as Marantaceae and a firm foundation for his taxonomic treatments of the genera in the New World. These contain very little emphasis on individual species, however. Eichler died while working on the Marantaceae for the *Flora Brasiliensis,* for which the account of this family was completed by Petersen, who also authored the brief and conservative treatment of the family in the first edition of the *Natürlichen Pflanzenfamilien.* Major generic reorganizations, especially among the taxa of the Old World, appeared in Schumann's treatment, which is the most recent revision of the family as a whole. Schumann recognized 26 genera, over twice the number in any of the other works mentioned above. Loesener updated Schumann's revision with a few alterations. In an effort to alleviate persistent confusion in the delimitation of genera, Andersson (1981a) reevaluated the neotropical genera using a wide array of characters and (some taxonomic changes notwithstanding) felt that his studies largely confirmed the validity of Schumann's genera.

Andersson's (1977, 1981a) proposed view of the early evolution of Marantaceae departs markedly from the emphases on a single character and on geographic distributions of the traditional tribal division. According to Andersson, the family probably originated in Africa (see Holttum for a contrary view); the five informal groups into which he sorted the New World genera hypothetically reflect distinct phyletic lines, each with its closest relatives in the Old World. Tomlinson (1961) failed to distinguish the traditional tribes anatomically, Williams & Harborne found them not to differ in distribution of flavonoid constituents, and Bisson *et al.* could find no cytological support for their maintenance.

Marantaceous inflorescences vary from congested capituliform or spicate arrangements to those with clustered subunits or infrequently individual flowers separated by elongated internodes. Spathelike, often colorful bracts are frequently arranged in imbricate spirals or distichous rows, or in some species they are widely separated. Growth pattern ranges between strongly monopodial and more or less sympodial. Branching may reach several orders of complexity (with repeated patterns or not) or may be nearly completely suppressed. As is

evident from two analyses of the architecture of inflorescences in Marantaceae (Eichler; Andersson, 1976), a fundamental uniformity underlies the confusing diversity.

Andersson's attempt to unify the terminology applied to the inflorescence is useful if it is borne in mind that the subunits that he recognized are not all constantly discernible throughout the family and that his naming of different levels within the inflorescence deemphasizes repetition in pattern. Like a vegetative branch, an axis in a marantaceous inflorescence begins with two short internodes, the first bearing a two-keeled prophyll (three-keeled in some flower pairs) and the other bearing an (often-suppressed) interphyll. As the result of repeated condensed basal branching, clusters of branches often falsely appear (e.g., in *Thalia dealbata*) to be axillary to a single bract. Monopodial axes bearing bracts typically subtending flower pairs or clusters of flower pairs were termed "florescences" by Andersson. The pairs of flowers are borne either singly or in often much-condensed sympodial arrangements ("florescence components"). Because the morphological nature of the flower pairs remains unsettled, they cannot be counted among taxonomic links to the Cannaceae, which also sometimes have paired flowers. Positions of associated foliar structures, symmetry and time of opening of the flowers, and supposed occasional manifestations of the missing terminal flower have been cited as evidence that the flowers of a pair in the Marantaceae are the two lateral members of an ancestrally three-flowered dichasium (see F. Müller, Eichler). Alternatively, the positions of the bracteoles in some specimens indicate one flower as lateral and the other as terminal (see Andersson, 1976). Kirchoff (1983b) concluded that in Marantaceae the members of a pair originate simply by division of an apical meristem.

Arils on seeds of Marantaceae appear to promote dispersal in at least three ways. Schumann (see also Humphrey) noted a correlation between dehiscent fruits and arillate seeds in the family and also stated that expansion of the aril can force apart the valves of such fruits. Eichler observed that the aril jutting from a partially dehisced fruit can help free it from the enclosing bracts. Bright coloration and deposits of lipids, which are at least sometimes present in marantaceous arils, point to a third role for these structures: the attraction of birds (Ridley) and ants. In a study of species of *Calathea* and several genera of ants, Horvitz & Beattie found that these insects sometimes (with variation between species) transport the seed by using the aril as a handle. The ants take the seed into their nest (perhaps a favorable, protected microsite for germination), use the aril as food (thus promoting germination), and bury the remainder of the seed in a refuse heap near the nest, where the effectively planted seed lies in a bed enriched by decaying organic waste and may be protected by the ants.

Prior to the tripping of the pollination mechanism, the style, confined by the cucullate staminode, develops tension, and the half-anther deposits pollen onto a specialized region below the stigma (FIGURE 3, k-13). One or two appendages rise from one margin of the cucullate staminode and arch across its concave side, thereby also extending over the style (FIGURE 3, g). As might be guessed from the appearance of these "triggers" (and as has been confirmed for some

species), their displacement by a suitable bee releases the springlike style from its confinement. When thus tripped, the style bends suddenly inward toward the callose staminode, which apparently functions in bracing the precisely arranged mechanism, in orienting the insect visitor, and as as anvil for the stroke of the style. The inward-moving stigma scrapes pollen from the insect, which is then at least sometimes smeared with sticky fluid from a glandular region on the style, followed by a dusting with pollen from the pad just behind. According to Kennedy, at least three genera of Marantaceae deposit the pollen on the proboscidial fossa, out of reach of the bee when cleaning itself. After pollination, the curled style and (when present) an appendage beyond the stigma (FIGURE 3, j-16) block further loss of nectar and/or autogamy. Euglossine bees, among which are pollinators of many orchids, are the principal pollinators of Marantaceae in the New World (Kennedy) but do not range into the southeastern United States (Michener). (Supplementary references on pollination are Andersson, 1981a; Eichler; Gris, 1859; Hildebrand; Knuth; H. Müller; Purseglove; and Schumann.)

The function of the peculiar chalazal canals in the seeds appears to be connected with the vascular tissue that defines their course early in development. Because the canals are closed off in the mature seed, they are unlikely to be conduits for air or water (Grootjen). Diverse inclusions of chalazal tissue in seeds of Zingiberaceae, Cannaceae, and Musaceae neither resemble nor initiate such canals.

Species of *Calathea*, especially *C. Allouia* (Aublet) Lindley, serve as minor sources of starch. Derivation of starch from *Maranta arundinacea* is discussed under that genus. The leaves of species of *Calathea* yield a wax of high quality (see Ayensu *et al.*). Several genera, among them *Maranta, Calathea* (e.g., *C. zebrina* (Sims) Lindley, zebra plant), *Ctenanthe* Eichler, and *Stromanthe* Sonder, are cultivated for their decorative foliage.

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1. **Thalia** Linnaeus, Sp. Pl. **2:** 1193. 1753; Gen. Pl. ed. 5. 3. 1754.

Usually tall (1–4 m in the southeastern United States), erect, large-leaved herbs of wet habitats. Glabrous or with soft hairs on axes of the inflorescence, bracts, floral parts, fruits, and leaves. Foliage leaves mostly or entirely basal, petiolate, homotropous. Inflorescences variably and usually richly branched, often with 3 or more axes falsely appearing to arise from a single node, the main axis clearly monopodial (*T. dealbata*), or forming pseudodichotomies with axillary branches (*T. geniculata*), the lateral branches with further bifurcations or not, the penultimate units conspicuous kinked or zigzag axes ("florescences" or "rachises") bearing a pair of flowers at each kink. Flowers of

FIGURE 3. **Thalia.** a–m, *T. geniculata:* a, portion of inflorescence, many flowers fallen, other flower buds enclosed within bracts (spathe and prophyll), cf. FIGURE 4, d, × ½; b, pair of tripped flowers (mirror images) enclosed within bracts (1 and 2), the continuing axis of inflorescence branch (unshaded circle) removed just above base of bracts, the

each pair laterally appressed and enclosed in a pair of unequal bracts, the smaller bract adjacent to the rachis (this bract the prophyll on the condensed shoot bearing the flower pair), the condensed shoot subtended by the larger, abaxial, boat-shaped bract (spathe), the spathes of several pairs often imbricate along the rachis while immature, spathes and prophylls both falling off with the fruits, leaving the rachis naked; other foliar organs in the inflorescence caducous or persistent. Corolla and androecium purplish or blue, sometimes pink [or white]. Sepals very small, distinct, hyaline. Corolla lobes distinct or nearly so, nearly equal to unequal, variably fused at the base with the androecium. Outer staminode constricted basally, showy and protruding, borne nearly abaxially to the rachis; cucullate staminode with 2 appendages, markedly connate with the callose staminode, this a very broad, bilobed hood provided at the edge adjacent to the fertile stamen (with which it is sometimes strongly connate) with an oblique, inward-jutting thickening; fertile stamen with its half-anther inserted laterally on a variably developed petaloid lobe. Gynoecium unilocular by abortion, with 1 fertile ovule; style twisted when triggered, free from the androecium, with an appendage derived from the initially adaxial rim of the stigmatic cleft projecting back into the flower after pollination. Fruit ellipsoid to subglobose, indehiscent, with a thin pericarp. Seed single, subglobose or ellipsoid, sometimes slightly flattened, with a smallish aril, the perisperm penetrated by 2 curved canals originating from a basal bifurcation and flanking the embryo. TYPE SPECIES: *T. geniculata* L. (Name commemorating Johann Thal, ca. 1542–1583(?), German physician and naturalist, who died after falling from a carriage.)

A cohesive, predominantly South American genus of seven or a few more species ranging from the southern United States, where two species are indigenous, to the West Indies, Argentina, and Uruguay, and represented throughout much of tropical (especially western) Africa by the often-mentioned "*Thalia Welwitschii* Ridley" and two other possible species (see Hepper, Koechlin, Gagnepain). As discussed below, it is likely that the widespread African populations resulted from human activity.

Said to be the largest-leaved herb native to the southeastern United States,

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floral parts numbered (see below for key to numbers), × 5; c, right-hand flower from "b," × 5; d–k, parts of flower from "c," × 3; l, diagrammatic cross section of ovary, oriented as in flower (c), the fertile ovule above with its micropyle toward the center septal nectary, the 3 septal nectaries and 2 empty, compressed locules below, × 12; m, fertile, basal ovule, the micropyle to lower left, × 12.

Key to floral parts in "b"–"k": 1, outer, lower bract (spathe) enclosing pair of flowers; 2, upper, inner bract (prophyll) enclosing pair of flowers; 3, upper, adaxial petal; 4, lateral petal (second lateral petal not visible); 5, outer staminode; 6–10, stamens of inner whorl—6, cucullate staminode (encloses style until pollination mechanism is triggered); 7, petaloid lobe, which together with callused lobe, 8, forms callose staminode, this connate with 9, fertile half-stamen, and 10, sterile half-stamen (the callose staminode connate at the other margin with 6); 11, lateral sepal; 12, inferior ovary; 13, pollen-bearing area of style (in "b" with pollen); 14, stigmatic cavity after pollination (note pollen); 15, style; 16, stylar appendage.

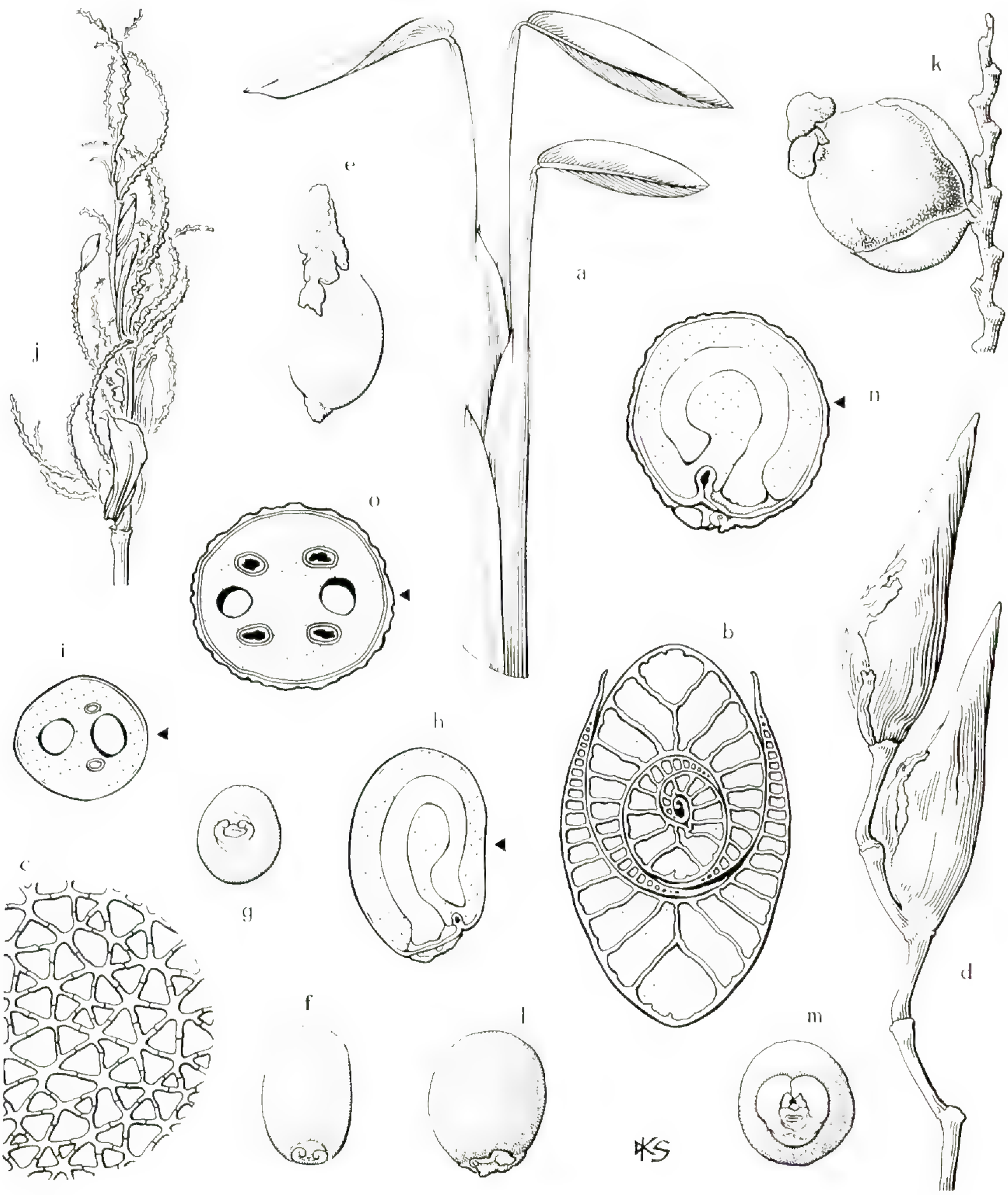

FIGURE 4. **Thalia.** a–i, *T. geniculata:* a, young leafy shoot (small)—note bladeless sheathing leaf at base, overlapping sheaths, and pulvinus between blade and petiole, × ¼; b, diagrammatic cross section of sheaths of 2 leaves and of a third, much younger leaf to show vertical plates of tissue (vascular bundles omitted) plus horizontal diaphragms (stippled), × 1¼; c, detail of a diaphragm from "b" to show connecting stellate cells with openings between, × 25; d, tip of inflorescence branch with 2 mature fruits, each enclosed by pointed outer and frayed inner bracts (spathe and prophyll, respectively), × 2; e, mature fruit with marcescent floral parts on top, × 2; f, seed, removed from fruit—note aril at base, × 2; g, base of seed to show aril, × 2; h, diagrammatic vertical section of seed (through arrow in "i"), thick part of aril to left at base, invagination of chalaza in black, perisperm stippled, curved embryo unshaded, outer seed coat heavy black line, inner seed coat unshaded, × 3; i, cross section of seed (oriented as in "h") at level of arrow in "h," showing seed coats, perisperm, embryo, and chalazal canals in perisperm, × 3. j–o, *T. dealbata:* j, inflorescence axes after fruits have fallen to show

Thalia geniculata L. (*T. divaricata* Chapman, *T. trichocalyx* Gagnep., *T. Welwitschii*) in this country is restricted to Florida but extends southward from Mexico and the West Indies approximately to Buenos Aires, Argentina. It is essentially absent from the drainages of the Amazon and upper Orinoco rivers. A distribution map of this species broadly defined with superposed highly variable but poorly correlated characters is provided in Andersson's revision of the "*Thalia geniculata* complex." The main problem tackled in this study was a taxonomic evaluation of the three African species of *Thalia,* the morphological divergence of which Andersson attributed to a "bottle neck effect" following supposed introduction of *T. geniculata* into Africa, possibly in the ballast of ships sailing from the Greater Antilles during the slave trade. As a consequence of this hypothetically recent and artificial separation, all African thalias were synonymized with *T. geniculata.* Andersson mentioned that plants fitting the original description of the tropical American *T. trichocalyx* grow in Florida, but he also included this species under *T. geniculata. Thalia geniculata* f. *rheumoides* Shuey, with red coloration on the leaves, inflorescences, and particularly the petioles, occurs in east-central Florida. Miège's report of $2n = 18$ for *T. geniculata* is based on material from Senegal; the provenance of the specimen used by Mahanty for a photograph of the chromosomes ($2n = 26$) is not specified.

Thalia dealbata Fraser ex Roscoe[9] (*T. barbata* Small), powdery thalia, $2n = 12$, grows on the Coastal Plain from South Carolina to Texas, in Oklahoma, Arkansas, and Missouri. This species differs most saliently from *T. geniculata* in having more compact, more rigid inflorescences with a less dichotomous aspect (internodes on the rachis 2–3 mm vs. 5–16 mm); smaller flowers and bracts (the spathe of each pair mostly less than 1.5 cm long vs. mostly longer); and the pruinose bloom for which it is named.

Delimitation of *Thalia,* which has no obviously close relatives, has been less troublesome than that of other genera of Marantaceae. Thalias are usually large herbs of wet places; they have homotropous leaves and paniclelike inflorescences with distinctive zigzag axes. The purplish flowers (ours) are borne in tight, bract-enclosed pairs without bracteoles; each has one conspicuous outer staminode, a very short corolla tube, minute sepals, a cucullate staminode with

[9]I have not seen an illustration of this species said by Roscoe to have been published by Fraser in Ic. Bot. Gard. Liverpool, probably in 1794.

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branching pattern—compare with "d" and with FIGURE 3, a, × ½; k, tip of inflorescence axis with a single fruit enclosed at base by prophyll and subtending spathe and tipped by marcescent floral parts, × 2; l, side view of seed, showing basal aril, × 2; m, base of seed to show aril, × 2; n, vertical section of seed (at level marked by arrow in "o"), showing thick part of aril to left, outer seed coat wavy, inner seed coat unshaded, basal invagination of chalaza in black, perisperm stippled, embryo unshaded (note that the 2 chalazal canals in perisperm branch from the invagination shown here), × 3; o, cross section of seed (at level marked in "n"), showing curved embryo (unshaded) in perisperm with parallel chalazal canals (much longer than in "i" and thus each cut twice) in black, × 3.

two (vs. usually one in other Marantaceae) appendages, a style with a large backwardly pointing appendage, and a unilocular ovary. The seed has a usually small aril and two (vs. usually one) curved chalazal canals. Andersson (1981a), confirmed the taxonomic isolation of *Thalia* and compared it with his "Myrosma group" of genera, *Halopegia* K. Schum., and *Hypselodelphys* (K. Schum.) Milne-Redhead, from all of which *Thalia* is distinguishable by the characterization above.

In the principal revision of *Thalia*, Schumann named four subgenera, which were retained by Loesener: EUTHALIA (containing our *T. dealbata*), ARTHROTHALIA (containing only *T. geniculata*), SAROTHALIA, and ANOMOTHALIA. In view of the small size of the genus (and because the first two subgeneric names contravene the ICBN, 1978) their continued recognition is of questionable value.

The two species of *Thalia* in the Southeast grow in or bordering ponds, streams, swamps, ditches, hammocks, and other wet places. Both flower from spring through autumn. Andersson (1981b), on the basis of observations in the field, thought plants of *T. geniculata* to be self compatible and geitonogamous. In the Southeast various insects reportedly visit flowers of *Thalia*; however, only carpenter bees (*Xylocopa*) are known to trigger the pollination mechanism (D. Austin, see acknowledgments). A gas-filled space between the seed and pericarp in *T. dealbata*, the canals in the perisperm, and the persistent waxy bracts may promote dispersal by water (see Grootjen).

Seeds of *Thalia* "*divaricata*" (*geniculata*) are reportedly eaten by ducks in Florida (McAtee). The inner portion of the boiled rootstock of *T. geniculata* is said to be suitable as food for humans (Morton, 1977). *Thalia dealbata* is sometimes cultivated in aquatic gardens.

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2. **Maranta** Linnaeus, Sp. Pl. **1:** 2. 1753; Gen. Pl. ed. 5. 2. 1754.

Perennial, or perhaps sometimes annual, erect [or prostrate] herbs of diverse habit, [some species without aerial stems or branched only basally,] when branched aerially the main shoot and axillary growth often divaricate-pseudodichotomous, usually terminating in inflorescences. Rhizome fleshy, with scale-covered stolons (*M. arundinacea*). [Glabrous or] with pale indument of variable length, texture, and density on stems, leaves, and ovary (*M. arundinacea*). Leaves homotropous [except in *M. Ruiziana* Koern.], separated by distinct internodes, variegated in some species, basal and cauline [or entirely basal], extremely diverse in shape (lanceolate to elliptic with the apex acuminate in *M. arundinacea*), the sheath sometimes extending to the pulvinus, this usually with an adaxial tuft of hairs. Inflorescences racemiform to diffusely branched, with the axillary and main shoots divergent (in the uncrowded inflorescences of *M. arundinacea* and some other species, the pattern of growth neither clearly monopodial nor clearly sympodial) [some species with compact, spicate branches ("florescences"), these actinomorphic or bisymmetrical]; flower pairs borne singly or in few-membered clusters ("florescence components"), each pair with a prophyll but no apparent interphyll, and no [or rudimentary] bracteoles, the pedicels of the 2 flowers and their common stalk of variable lengths, 1 flower apparently terminal and on a longer pedicel, the other apparently lateral and on a shorter pedicel; bracts sheathing, persistent or caducous. Flowers white [to bluish, purplish, or otherwise]. Sepals free, equal, acute, fibrous. Corolla with a usually long tube, this usually gibbous at the base and bent and adnate to the androecium and style; corolla lobes subequal, cucullate at the apex. Outer staminodes 2 (or 3), unequal, conspicuous and flaglike (obovate and usually emarginate in *M. arundinacea*); cucullate staminode with 1 lateral appendage; callose staminode often 2-lobed; fertile stamen with the petaloid half basally connate with and apically wrapped around the cucullate staminode (*M. arundinacea*); pollen grains inaperturate or possibly

sometimes uniaperturate. Ovary 1-locular by abortion with 1 fertile ovule; stigma in a usually funnel-shaped hollow formed by a pair of lips at the end of the style. Fruit indehiscent or sometimes 3-valved, ellipsoid, 3-angled in transverse aspect, with 1 seed (some cultivars of *M. arundinacea* seedless). Seed rectangular in longitudinal view, triangular in transverse view, with a pale yellow aril; perisperm canal straight, bifurcate apically. TYPE SPECIES: *M. arundinacea* L. (the only species included by Linnaeus in the *Species Plantarum*). (Named for the botanist Bartolommeo Maranta, died ca. 1560, a native of Venosa, Italy.)

About 20 species, many of them poorly defined, in four questionable subgenera, indigenous to tropical America, especially Brazil, with *Maranta Friedrichsthaliana* Koern. endemic to Costa Rica and *M. arundinacea* and *M. divaricata* Roscoe (= *M. arundinacea*?) also in Central America. No species is clearly native to the West Indies (see Howard for comments on three species collected in the Lesser Antilles). Since *M. arundinacea* has escaped cultivation and become naturalized sporadically in warm portions of both the Old and New Worlds, its original distribution can only tentatively and vaguely be stated as tropical South America and possibly Central America. Whether or not this species preceded Europeans in the West Indies is uncertain; it was clearly under cultivation there in the 1600's (cf. Hodge & Taylor, Purseglove, Sturtevant). Cultivated at least as far north as northern Florida, *M. arundinacea* has evidently become a minor element in the flora of South Florida. Small (p. 361) described it as occurring on "hammocks and moist soil, S. pen. Fla.," and in a few more recent publications (Ward; Morton, 1977), this species is accepted as growing without cultivation in Florida. However, its meager representation in other checklists and consulted sources should be noted. This representative of subg. MARANTA (divaricately branched; bracts few, not imbricated, convolute around the axis; flower pairs on long pedicels) has uncrowded, highly branched growth, leaves with long-attenuate apices, white flowers with the ovaries glabrous or pubescent on the corners, and thickened stolons.

In 1859 and 1862 Koernicke envisioned *Maranta* as a broadly circumscribed genus made up of four "Untergattungen" or (in his second paper) sections: EUMARANTA, STROMANTHE (Sonder) Koern., SARANTHE Regel & Koern., and XOROLEPIS Koern. Eichler retained part of Koernicke's sect. EUMARANTA as the genus *Maranta* and sorted the remainder of the former genus, with changes in the groupings, chiefly into the genera *Stromanthe* Sonder, *Saranthe* (Regel & Koern.) Eichler, and *Ctenanthe* Eichler, all of which have been maintained as genera with further adjustments in delimitation in subsequent revisions. Using characters concerned with the form and arrangement of bracts, coloration of leaves, habit, and structure of the inflorescence, Schumann named four new subgenera under *Maranta*: AUTOMARANTA (i.e., MARANTA), KOERNICKEA, CALATHEASTRUM, and FRIEDRICHSTHALIA.

Andersson (1981a), who rejected Schumann's subgenera, placed *Maranta* alongside *Monophyllanthe* K. Schum. to form his informal "*Maranta* group" and indicated that the two genera perhaps ought to be merged. Species of the

Maranta group tend to have long floral tubes; fibrous, acute sepals; the cucullate staminode with only one appendage; a funnel-shaped stigmatic orifice; flower pairs with elongate axes and without interphylls and (usually) bracteoles; an apically bifurcate perisperm canal in the solitary, mature seed; and usually homotropous leaves. *Maranta* differs from *Monophyllanthe*, according to Andersson, in having two equally developed outer staminodes (vs. one staminode reduced or absent) and in details of habit. Andersson concluded that the closest affinities of the *Maranta* group are with the African genus *Marantochloa* Brongn. & Gris, which differs in having three fertile ovules, instead of only one.

Saranthe, *Ctenanthe*, and *Stromanthe*, placed in the "*Myrosma* group" by Andersson, are evidently not strongly differentiated either from each other or from the *Maranta* group. With exceptions, these genera differ from *Maranta* in having proportionately shorter floral tubes, usually shorter internodes and more frequent bracteoles in the flower pairs, and a tendency to have the bracts on branches of the inflorescence (florescences) in a monosymmetric arrangement (vs. radially or bilaterally symmetrical). *Ctenanthe* and *Stromanthe* differ further from most species of *Maranta* in having antitropous leaves.

Any generalization about cytology in *Maranta* is hampered by reports on dubiously identified specimens, even at the generic level, and by substantial cytological heterogeneity. Vouchered survey work is needed. From the information we have, it appears that somatic chromosome numbers range between 18 and 52. (A diploid number of 8 was reported for *M.* "*nitida-picta*"—see Venkatasubban.) As judged from very limited data, cytological differences between species of *Maranta* extend to the lengths of chromosomes and the positions of centromeres. In *M. arundinacea*, $2n = 18$ (46, 48, 52 also reported), Satô encountered two long pairs of chromosomes with submedian centromeres, a medium-long pair with median centromeres, five short pairs (one with submedian centromeres, the remaining four with subterminal), and one very short pair with terminal centromeres.

According to one account in the collection of correspondence concerning *Maranta arundinacea* (Anonymous, 1893), the name "arrowroot" may have originated from the Carib *ara-ruta*, "mealy root"; alternatively, the name may stem from use of the rhizome in treating wounds from poisoned arrows. "Arrowroot" has become generalized to other plants with starch-yielding rhizomes, such as *Canna edulis*.

Produced in tropical countries worldwide, chiefly on the West Indian island of St. Vincent, true arrowroot starch is extracted from the tough, fibrous rhizomes of *Maranta arundinacea*. Easily digestible, the starch is particularly valuable for feeding infants and persons with special dietetic requirements. Additionally, it is or has been used like other starches, such as for starching laundry, in glue, and in the preparation of powders for the skin. Among the many medicinal uses are application internally and externally to counteract poisons and in poultices to treat various dermatological afflictions. Species of *Maranta*—among them *M. bicolor* Ker-Gawl. and the prayer plants, *M. leuconeura* Morren (including var. *erythroneura* Bunting)—are popular in homes and greenhouses for their decorative, sometimes variegated foliage. At least

one cultivar of *M. arundinacea* has variegated leaves. (Additional references concerned with uses for *Maranta* are Ayensu, Hamilton, Hodge & Taylor, Morton (1977), Neal, Purseglove, and Sturtevant.)

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ADDENDUM

After this paper was completed, a specimen of *Thalia geniculata* cultivated indoors at the Arnold Arboretum flowered for the first time, allowing us to make the following observations.

In bud, the anther deposits large (ca. 100 μm in diameter when fresh) pollen grains onto the style within the cucullate staminode. Possibly functioning as a trigger, the stylar appendage in the open untripped flower rises as a steep uphill floor at the entrance of the floral tube. The pollination mechanism is extremely sensitive and is easily sprung by various minor disturbances. After being (artificially) triggered, the style twists and comes to rest blocking the floral tube, with the pollen-bearing portion against the outside of a pouch formed by a membrane extending between the callose staminode and the thickened lobe on it. Presence of numerous pollen grains in the stigmatic cleft suggests that self-pollination can occur in the absence of a pollinator during the stroke of the style. Consistent with this possibility, artificially triggered flowers readily formed fruit when bagged in bud or immediately following triggering. (It was impossible to bag flowers singly.) I have not ruled out the presence of pollen in the stigmatic cleft prior to release of the style, other forms of autogamy, or apomixis.

A MONOGRAPH OF DIPHYLLEIA (BERBERIDACEAE)

TSÜN-SHEN YING, SUSUMU TERABAYASHI, AND DAVID E. BOUFFORD

DIPHYLLEIA Michaux is one of approximately 120 genera with members exhibiting the classic eastern Asian–eastern North American disjunction pattern. It was one of the first examples of this pattern that Asa Gray (1859) pointed out when he listed *D. grayi* F. Schmidt (as *D. cymosa* Michaux) as one of a number of taxa restricted to these two widely separated areas. Three species of *Diphylleia* (*D. cymosa, D. grayi,* and *D. sinensis* H. L. Li) are presently recognized, each occurring in separate, disjunct regions. Despite this well-known distribution pattern and the interest it has generated, there have been relatively few detailed studies of the taxa involved. The following account is an attempt to bring together the scattered information on *Diphylleia* and to point out areas where further studies might result in a better understanding of this disjunction pattern.

Floristically, eastern Asia and eastern North America are two of the largest and most complex relictual areas for the once-widespread Mixed Mesophytic Forests that circled the globe at middle and high latitudes in the Northern Hemisphere during the Tertiary (Wood, 1972). These forests and their floras become extinct in large intervening areas during the orogenies and climatic deterioration of the late Tertiary and the glaciations of the Pleistocene. *Diphylleia,* unknown in the fossil record, can be inferred from its present occurrence with dominant relictual Tertiary woody genera with well-documented fossil histories (e.g., *Fagus* L., *Liriodendron* L., *Magnolia* L., *Cercidiphyllum* Sieb. & Zucc., *Cornus* L. subg. *Thelycrania* Endl., *Tsuga* Carr.) to have been a member of these forests, even though the components of the present forest may have had very different histories. Although it might be argued that the current distribution of *Diphylleia* is the result of long-distance dispersal, it seems more likely that the berry fruits enabled a more continuous and widespread distribution during the Tertiary by dispersal over shorter distances. The present localized distribution of *D. cymosa* in the southern Appalachian Mountains of the southeastern United States is unexplainable. In cultivation plants of this species are able to grow far north of their present range. It may be that they are unable to compete in nature with other, better-adapted plants farther north, or that they have been unable to bridge intervening unsuitable habitats since the melting of the last continental glaciers to reach the seemingly suitable habitats occurring outside of their present range.

In addition to *Diphylleia,* other genera and species of Berberidaceae *s.l.* (*Caulophyllum* Michaux, *Jeffersonia* Bartram, *Podophyllum* L., and close relatives of *Berberis canadensis* Miller) are well known for their discontinuous

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distribution in eastern North America and eastern Asia. With the exception of *Berberis*, these genera are all perennial, rhizomatous herbs that grow in rich, moist soils in mixed deciduous forests.

ECOLOGY

The three species of *Diphylleia* occupy similar habitats in the eastern United States, Japan, and China. All are found on gentle to steep slopes in seepages or along streams. They grow in brown forest soils or podzols that are rich in organic matter and characteristically acidic (pH 4.5–7.0 for *D. sinensis* in the Shennongjia Forest District in central China (*Shennongjia Bot. Exped. 10276* and *25107*); 4.0–5.8 for *D. cymosa* in samples from Watauga County, North Carolina (*Boufford & E. W. Wood 16310*), and Rabun County, Georgia (*Boufford & E. W. Wood 17033*), in the United States). The plants are found in cool-temperate, mixed-deciduous broad-leaved forests, in mixed-deciduous broad-leaved and coniferous forests, and in nearly pure coniferous forests at high altitudes or latitudes. On Mount Jinfu Shan in southeastern Sichuan Province, *D. sinensis* is sometimes found growing in bamboo thickets. Plants characteristically associated with *Diphylleia* in each of the three disjunct regions are listed in TABLE 1. Hara (1959), Numata *et al.* (1972), and Numata (1974), without referring specifically to *D. grayi*, have discussed some of the associations in which it occurs in Japan.

Due to its use as a medicinal plant and to the destruction of its habitat, *Diphylleia sinensis* is becoming increasingly scarce. In Japan and the United States, however, large areas where *Diphylleia* grows are under protection in national forests and national parks, and the plants are in no danger of extirpation.

ECONOMIC IMPORTANCE

In China, where *Diphylleia sinensis* has long been used as a folk remedy, the rhizomes are collected during the summer or fall, cut into slices, and dried in the sun. An infusion of the rhizomes has been employed in the treatment of injuries from falls; chewing and swallowing the rhizome has been a remedy for stomach trouble. The rhizome, however, contains poisonous substances, and care should be taken in using it; it should not be taken during pregnancy (Fu, 1976; Anonymous, 1974). It has also been reported (Anonymous, 1974) that the rhizome has been employed in treating lumbago, rheumarthritis, "menoxenia," and gynecologic ailments, and that the roots are useful in lowering fever, detoxification, dissolving blood clots, and improving circulation.

Diphylleia grayi is occasionally cultivated as an ornamental plant in Japan. Lloyd and Lloyd (1887, p. 120), commenting on *D. cymosa*, stated "It is not an article of commerce, there being no demand for it."

CHEMISTRY

Murakami and Matsushima (1961) investigated chemical compounds in the rhizomes of *Diphylleia grayi*. They reported podophyllotoxin, picropodophyl-

lin, β-apopicropodophyllin, kaempferol, quercetin, diphyllin, and an additional substance that they assumed to have a 4-arylnaphthalene skeleton. They believed that the constituents picropodophyllin and β-apopicropodophyllin were formed from podophyllotoxin during separation.

Lloyd and Lloyd (1887) noted that after evaporation, alcohol extractions of the rhizomes of *Diphylleia cymosa* produced a bitterish, acrid-tasting resin similar to that obtained from *Podophyllum peltatum*. They also reported that *Diphylleia* extracts had no medicinal properties, in contrast to those of *Podophyllum*, and (p. 120) "careful investigations demonstrated that no trace of an alkaloid or other interesting constituent existed in the plant."

More recent investigations by Kimura (1963) revealed that extracts of *Diphylleia grayi* contain substances similar to colchicine and podophyllin that produce an antimitotic effect on cancer cells of MTK-sarcoma III, Yoshida-sarcoma, and Ehrlich ascites carcinoma: the cells die without progressing beyond metaphase, thereby causing regression in tumors. Toyokuni and Toyokuni (1964) used this evidence as a basis for a classification of the Podophyllaceae in which they recognized two subfamilies. One, the Podophylloideae, contains podophyllin or podophyllinlike substances that inhibit tumors; the other, the Glaucidioideae, contains no podophyllinlike substances and has no effect on tumors. They considered the Podophylloideae to contain two genera, *Podophyllum* (nine species) and *Diphylleia* (*D. cymosa* and *D. grayi*). The sole member of their Glaucidioideae is *Glaucidium palmatum* Sieb. & Zucc.

ANATOMY

Material used in this study consisted of flowers, buds, and vegetative parts of *Diphylleia cymosa* and *D. grayi*, and fruiting peduncles and pedicels of *D. sinensis*, all preserved in FAA. Voucher specimens are cited in APPENDIX 1. Methodology was the same as in Terabayashi (1983). For a more detailed description of the anatomy of *Diphylleia*, that paper should be consulted.

RHIZOME AND ROOT

Kumazawa (1930) discussed the anatomy of the rhizome and root in *Diphylleia grayi*. Our study confirms Kumazawa's findings and shows the root and rhizome anatomy of *D. cymosa* and *D. grayi* to be similar. Secondary xylem elements and an interfascicular cambium are not produced, and the phellogen in the rhizome is subepidermal in origin. The roots of *Diphylleia* are adventitious and about 1 mm in diameter. The stele of the roots in *D. grayi* and *D. cymosa* is usually tetrarch (see FIGURE 1), with secondary xylem elements rarely produced. According to Zhong Guo Yixui Gexui Yuan Yowu Lianjuoso (1979) the root of *D. sinensis* differs from those of the other two species in having a pentarch stele.

STEM

Studies of Harvey-Gibson and Horsman (1919), Himmelbaur (1913), Kumazawa (1930), and Worsdell (1908) showed that *Diphylleia* is among a small number of dicotyledonous genera having the monocotyledonous feature of

TABLE 1. **Plants characteristically associated with Diphylleia.***

CHINA **D. sinensis**	JAPAN **D. grayi†**	UNITED STATES **D. cymosa**
Abelia dielsii		
Abies fargesii	*Abies mairesii*	*Abies fraseri*
	Abies veitchii	
Acer caudatum	*Acer rufinerve*	*Acer pensylvanicum*
var. *multiserratum*	*Acer tschonoskii*	*Acer saccharum*
Acer tetramerum	*Acer ukurunduense*	*Acer spicatum*
Actaea asiatica	*Actaea asiatica*	*Actaea pachypoda*
		Aesculus octandra
		Arisaema triphyllum
Asarum caudigerum		
Athyrium fallaciosum	*Athyrium* spp.	*Athyrium asplenioides*
Athyrium filix-femina		
Betula albo-sinensis	*Betula ermanii*	*Betula alleghaniensis*
var. *septentrionalis*		*Betula lenta*
Betula fargesii		
Cacalia roborowskii	*Cacalia adenostyloides*	*Cacalia muhlenbergii*
Cardamine engleriana		*Cardamine clematitis*
Caulophyllum robustum	*Caulophyllum robustum*	*Caulophyllum thalictroides*
Chrysosplenium micro-		
spermum		
Cimicifuga foetida		*Cimicifuga racemosa*
Circaea alpina	*Circaea alpina*	*Circaea alpina*
subsp. *imaicola*	subsp. *alpina*	subsp. *alpina*
Clintonia udensis	*Clintonia udensis*	*Clintonia umbellulata*
	Coptis trifolia	
		Disporum lanuginosum
Dryopteris sinofibrillosa	*Dryopteris austriaca*	*Dryopteris austriaca*
	Dryopteris crassirhizoma	*Dryopteris intermedia*
	Fagus crenata	*Fagus grandifolia*
	Glaucidium palmatum	
Kingdonia uniflora		
	Kinugasa japonica	
Ligularia stenocephala		
	Lindera umbellata	*Lindera benzoin*
Liriodendron chinensis		*Liriodendron tulipifera*
Lonicera kungeana		
		Magnolia acuminata
		Magnolia fraseri
	Oxalis acetosella	*Oxalis acetosella*
Panax pseudo-ginseng		
var. *bipinnatifidus*		
Paris thibetica	*Paris polyphylla*	
	Paris tetraphylla	
Peracarpa carnosa	*Peracarpa carnosa*	
var. *circaeoides*	var. *circaeoides*	
Picea wilsonii	*Picea jezoensis*	*Picea rubens*
	Plagiogyria matsumureana	
Polygonatum roseum		*Polygonatum pubescens*
	Polystichum retrorso-	*Polystichum acrostichoides*
	paleaceum	
Prunus gracilifolia	*Prunus grayana*	*Prunus serotina*
Pseudocystopteris spinulosa		

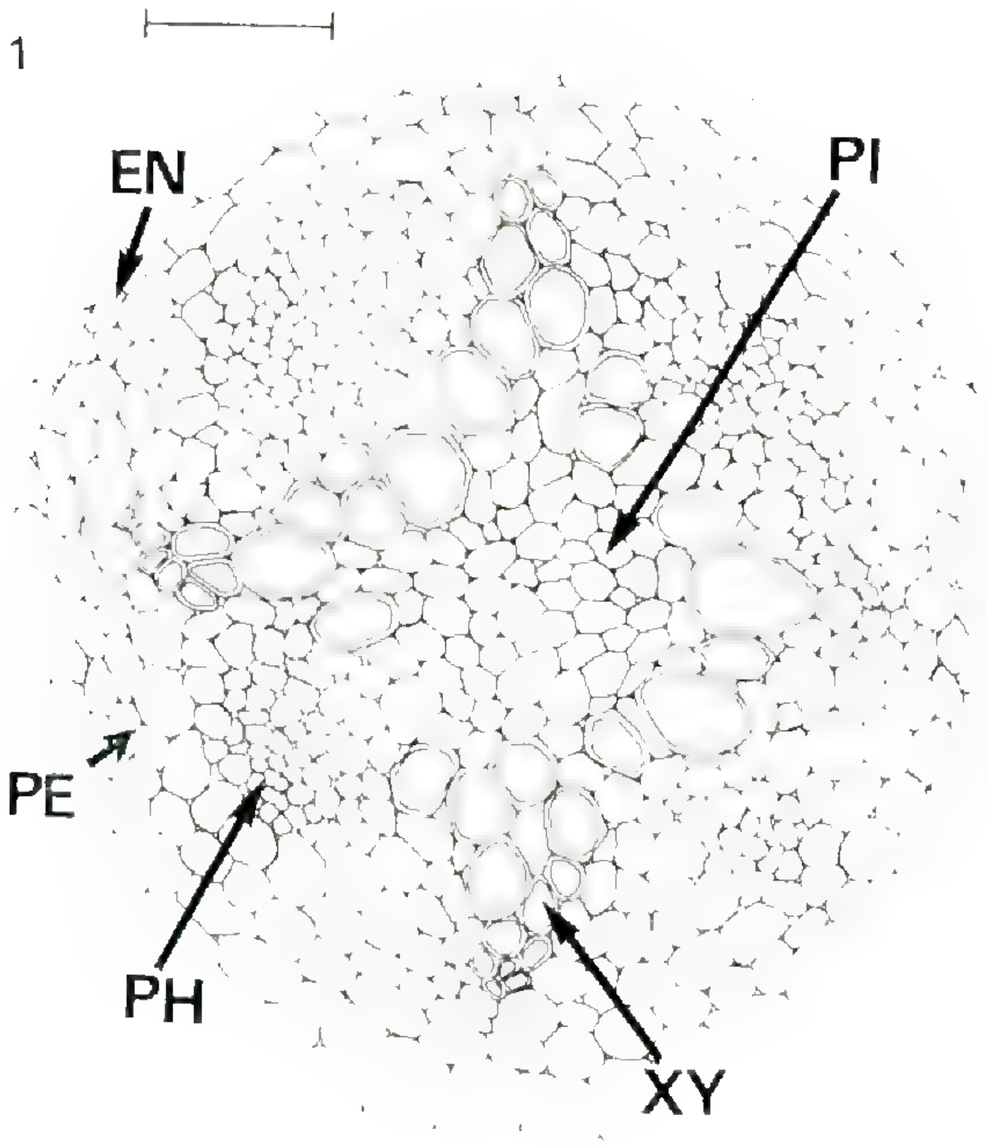
TABLE 1 *(continued).*

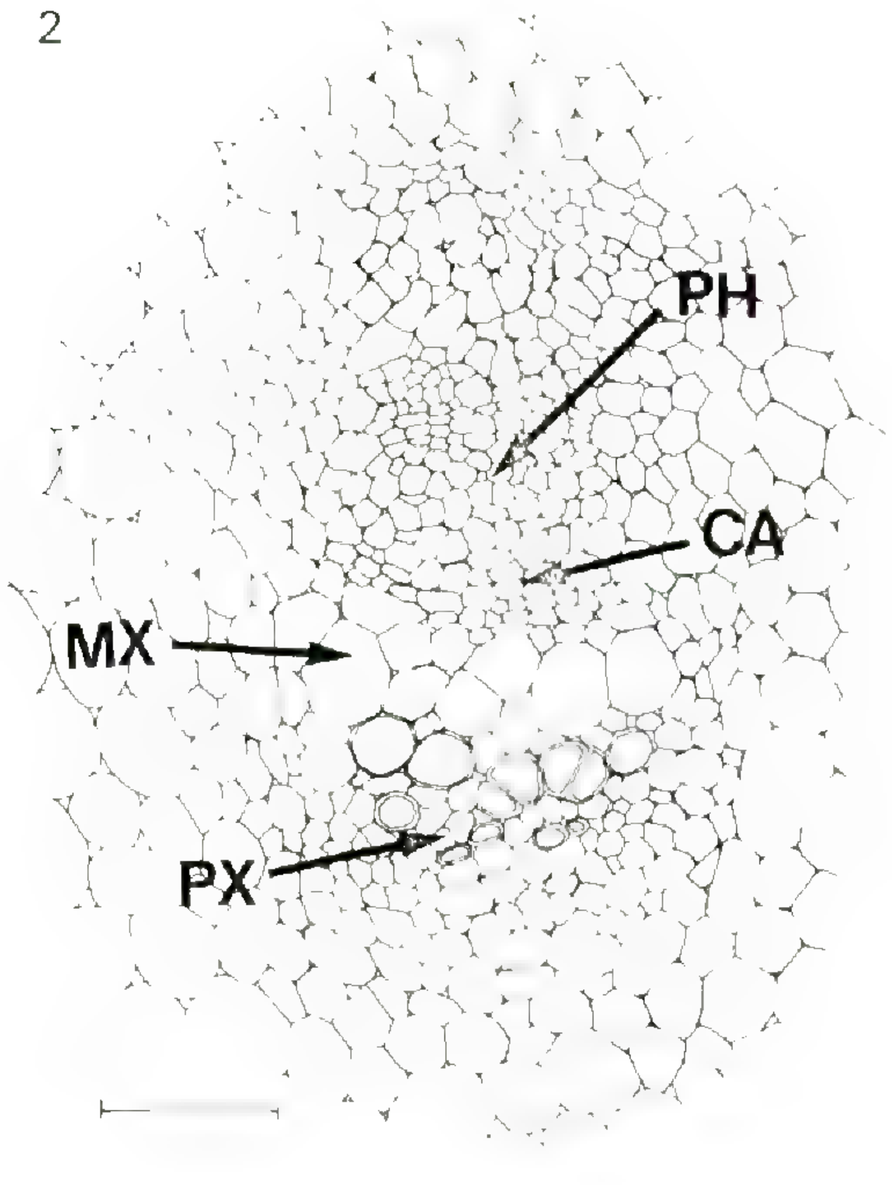
CHINA **D. sinensis**	JAPAN **D. grayi**†	UNITED STATES **D. cymosa**
Rhododendron concinnum		*Rhododendron maximum*
Rhododendron fargesii		*Rhododendron catawbiense*
Rhododendron purdomii		
Ribes glaciale		*Ribes rotundifolia*
Rosa omeiensis		
Salix cathayana		
		Saxifraga micranthidifolia
Schisandra incarnata		
Schisandra sphenanthera		
Sinarundinaria indica		
Smilacina henryi		*Smilacina racemosa*
Smilacina japonica	*Smilacina japonica*	
Sorbus koehneana		
	Streptopus streptopoides var. *japonicus*	*Streptopus roseus*
Thalictrum ichangense		*Thalictrum clavatum*
Thalictrum przewalskii		
Tiarella polyphylla	*Tiarella polyphylla*	*Tiarella cordifolia* subsp. *cordifolia*
		Tilia americana (incl. *T. heterophylla*)
	Trautvetteria japonica	*Trautvetteria caroliniana*
Trillium tschonoskii	*Trillium smallii*	*Trillium erectum*
		Trillium grandiflorum
		Trillium vaseyi
Triosteum himalayanum		
Tsuga chinensis	*Tsuga diversifolia*	*Tsuga canadensis*
Vaccinium japonicum var. *sinensis*	*Vaccinium japonicum* var. *japonicum*	*Vaccinium erythrocarpum*
Viburnum betulifolium		
Viola acuminata		

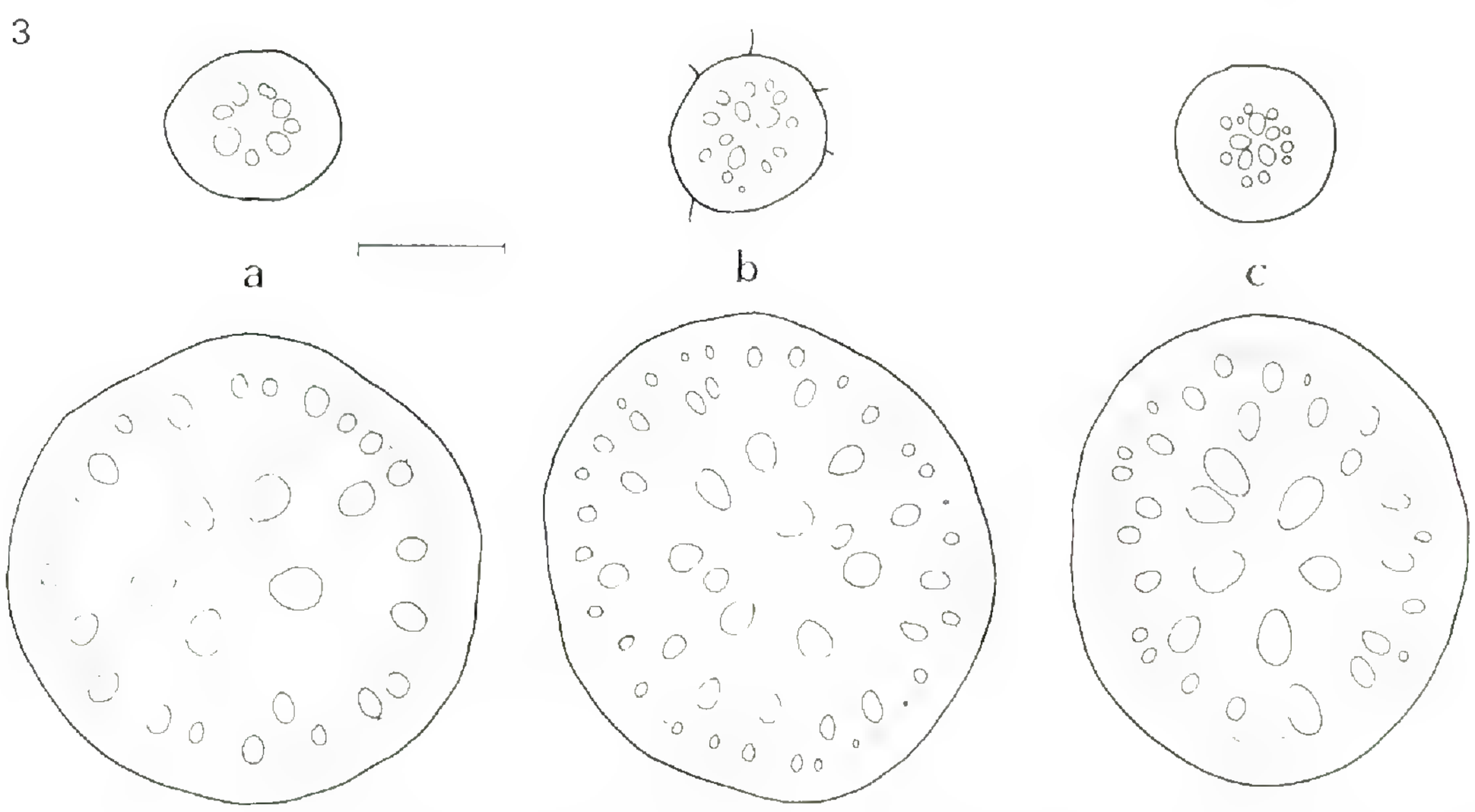
* Author names have been omitted to save space.

† Partially from Hara (1959), Numata (1974), and Numata *et al.* (1972).

scattered vascular bundles in the stem stele. The aerial stem in all three species is about 10 mm in diameter and contains 70 to 80 scattered vascular bundles in the portion below the leaves; between 40 and 50 vascular bundles occur in the internodal region (see FIGURE 4). The interior bundles are larger and mature earlier than those near the periphery. A sclerenchymatous ring, in which the phloem of the outer small bundles is embedded, is found near the periphery of the mature aerial stem. Kumazawa (1930, 1932) reported that the inner bundles give rise to the leaf traces in *D. grayi*. The same is true in *D. cymosa*. After the separation of traces to the upper leaf, a rearrangement of the vascular bundles occurs so that there are two concentric circles of vascular bundles in the peduncle. This configuration persists through the pedicel in *D. grayi* and *D. sinensis*, but in *D. cymosa* one circle is lost during branching of the inflorescence, so the stele of the pedicel consists of only a single circle of vascular bundles (FIGURE 3). Where two circles of vascular bundles occur, the bundles







FIGURES 1–3. Cross sections. 1, *Diphylleia grayi*, root, showing tetrarch stele (EN, endodermis; PE, pericycle; PH, phloem; PI, pith; XY, xylem; scale = 0.1 mm). 2, *D. grayi*, vascular bundle in stem (MX, metaxylem (slightly immature in this sample); PX, protoxylem; PH, protophloem; CA, inactive cambium; scale = 0.1 mm). 3, vasculature of peduncles (below) and pedicels (above), scale = 1 mm; a, *D. cymosa* (note single circle of vascular bundles in pedicel); b, *D. grayi*; c, *D. sinensis*.

in the inner circle are larger than those of the outer. A cross section of a single vascular bundle in the stem of *D. grayi* is shown in FIGURE 2.

LEAF

The petiole of *Diphylleia* is stemlike, with scattered vascular bundles. There are 40 to 50 vascular bundles in the petiole of the lower leaf, and 20 to 30 in

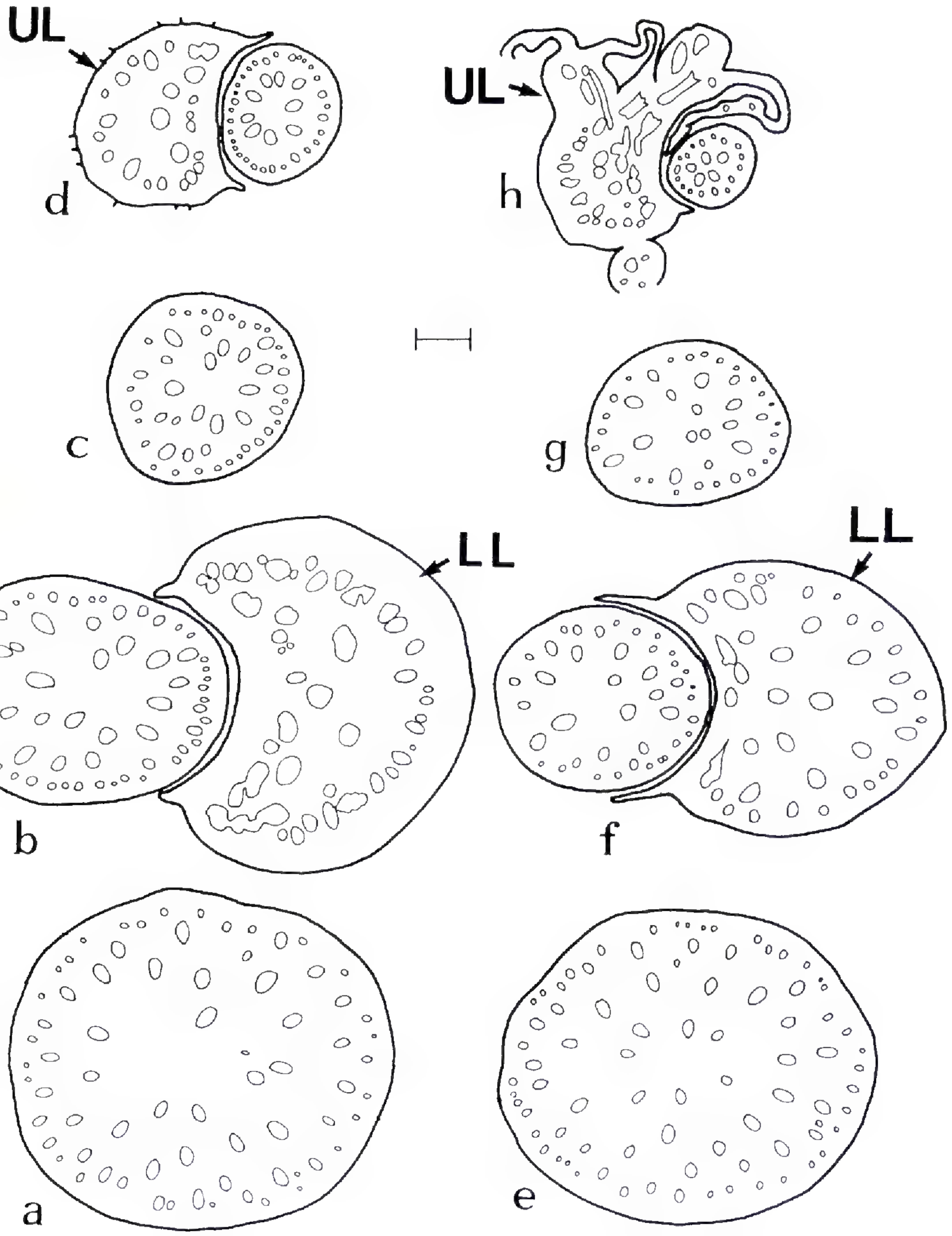


FIGURE 4. Cross sections of aerial shoots of *Diphylleia* showing vasculature: a–d, *D. cymosa*; e–h, *D. grayi* (note sessile upper leaf in h). a and e, near ground level; b and f, just above node of lower leaf; c and g, internodal region; d and h, just above upper leaf. Scale = 1 mm.

that of the upper leaf. The petioles are round in cross section from about the middle upward, but the lower portion shows dorsiventrality in both external and internal morphology (FIGURE 4).

The anatomy of the leaf blades in *Diphylleia grayi* and *D. cymosa* was studied by Oganozova (1974), who found the mesophyll of *D. cymosa* to be ca. 0.07 mm thick, with the palisade layer one cell thick and the spongy tissue four

cells thick. He reported the number of stomata of the lower epidermis to be 25 per mm^2 in *D. cymosa* and 24 per mm^2 in *D. grayi*.

The leaves are folded umbrellalike in bud in *Diphylleia*, as they are in *Podophyllum* and *Dysosma* Woodson. Kumazawa (1937) indicated that in *Podophyllum* and *Dysosma* the summit of the folded leaf is at the position of attachment to the petiole, although in *Diphylleia* the fold in the leaf is above the point of attachment.

FLOWER

Terabayashi (1983) examined the floral vasculature of *Diphylleia cymosa* and *D. grayi* in detail. Unfortunately, in both his study and ours flowering material of *D. sinensis* was unavailable for comparison. In *D. grayi* the double circle of vascular bundles in the pedicel continues into the receptacle; the inner circle contains the main bundles. In *D. cymosa*, where the pedicellate stele is composed of a single circle of vascular bundles, an outer circle of bundles arises from the stelar bundles at the lowest level of the receptacle, so the receptacle contains the two circles of bundles as in the peduncle and stem. No major differences are seen in the trace patterns to the sepals, petals, stamens, and pistils in the two species. The traces to the outer sepals originate mainly from the outer circle of vascular bundles, while those to the inner sepals, petals, and stamens usually derive from adjacent bundles in the inner circle. In exceptional cases, weak bundles from the outer circle may fuse with the petal traces. The pistil is traversed by a few ventral bundles and a dorsal bundle that extends to the stigmatic region. The ovary wall is covered by a network of veins. The ovular traces arise from ventral bundles, while those in the placental region originate from bundles other than ventral bundles.

Chapman (1936) and Kaute (1963) studied pistil anatomy in *Diphylleia* and interpreted the pistil as being pseudomonomerous. Kaute (1963) observed abnormally dimerous pistils with a single locule but with two placentas in *D. cymosa*. Such abnormally dimerous pistils were also observed in *D. grayi* by Terabayashi in this study. The monomerous pistil in *Diphylleia* may have been derived from a dimerous pistil through reduction.

EMBRYO

In *Diphylleia cymosa* the ovule is bitegmic and crassinucellate; embryo sac formation is of the Polygonum type, and pollen formation is simultaneous (Mauritzon, 1936). Terabayashi found the ovular morphology and embryo sac formation in *D. grayi* to be the same as in *D. cymosa*. The seed coat of *D. grayi* is exotestal, according to Corner's terminology (Corner, 1976; Takhtajan & Melikian, 1972).

SEEDLING

The seedlings of *Diphylleia* are characterized by long "cotyledonary tubes" (Himmelbaur, 1913; Terabayashi, in prep.). The cotyledon is two-parted, with the "cotyledonary tube" and an orbicular lamina. The plumule is hypogeal. The seedling does not produce foliage leaves during the first year after germination. The stele in the radicle and hypocotyl is diarch.

CYTOLOGY

The number and karyotype of the chromosomes of *Diphylleia grayi* are well known. Counts of $2n = 12$ have been reported in this species by Kurita (1956), Kuroki (1967), Matsuura and Suto (1935), Miyagi (1930), S. Noda and Fujimura (1970), Noguchi and Kawano (1974), and Soeda (1942). The anomalous count of $2n = 16$ attributed to Lee (1967) is in error. Lee reported $2n = 16$ for *Caulophyllum robustum* Maximowicz; this count was later mistakenly reported as being for *D. grayi* by Noguchi and Kawano (1974). As far as we have been able to determine, Lee did not examine chromosomes in *Diphylleia*.

The single report (Langlet, 1928) of $2n = 12$ for *Diphylleia cymosa* was determined from plants in cultivation in Europe. Langlet considered *Diphylleia* to be monotypic, with *D. cymosa* as the sole species. Although it can be assumed that the material he was working with—and probably the species in cultivation in Europe at the time—was *D. cymosa*, there is no way to prove this. Langlet did not cite vouchers for his cytological studies, and we saw no specimens collected or annotated by him among those that we examined. Until Langlet's report can be verified, it seems best not to attribute counts to *D. cymosa*.

No counts have been made of the Chinese *Diphylleia sinensis*. Chromosome counts of *Diphylleia* are summarized in TABLE 2.

Kurita (1956), Kuroki (1967), S. Noda and Fujimura (1970), and Noguchi and Kawano (1974) reported similar karyotypes in plants of *D. grayi* collected from widely separated populations in Hyogo, Iwate, and Tochigi prefectures, Japan. All reported two pairs of large (length 10.7–15.5 μm; all measurements from Kurita, 1956, and Kuroki, 1967), metacentric chromosomes, one pair of medium (length 9–11.1 μm), submetacentric chromosomes, and one pair of medium (length 8.4–10.8 μm), submetacentric chromosomes with a constriction at the midpoint of the shorter arm (Noguchi and Kawano (1974) reported the constriction to be at the distal end of the short arm, but their illustration shows it to be more nearly medial). Of the two remaining pairs, all of the authors reported them as being small (length 6.3–7.6 μm), with one pair being telocentric and the other having a subterminal constriction. Soeda (1942) found an additional constriction on the short arm of the small, telocentric chromosome, but none of the other authors mentioned this.

S. Noda and Fujimura (1970) also examined mitosis in developing seeds. In the plants in their study, they found that fruit-set was about 60 percent, but only 21.1 percent of the ovules developed into mature seeds. They (pp. 2549, 2551) attributed this high sterility to an ". . . asynchronization of mitosis" that they observed in endosperm tissue.

PALYNOLOGY[1]

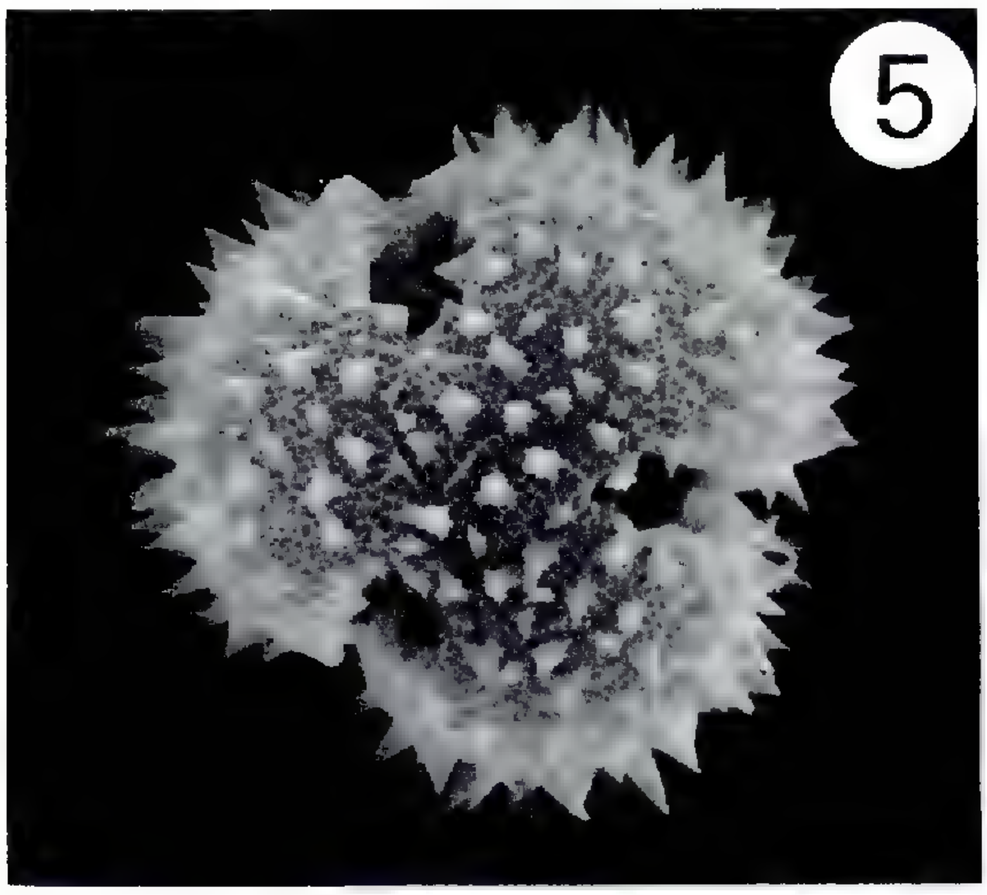
Pollen samples were collected from unopened buds or young flowers on herbarium specimens (see APPENDIX 2 for vouchers) of three sheets each of *Diphylleia cymosa*, *D. grayi*, and *D. sinensis*. The samples were acetolyzed

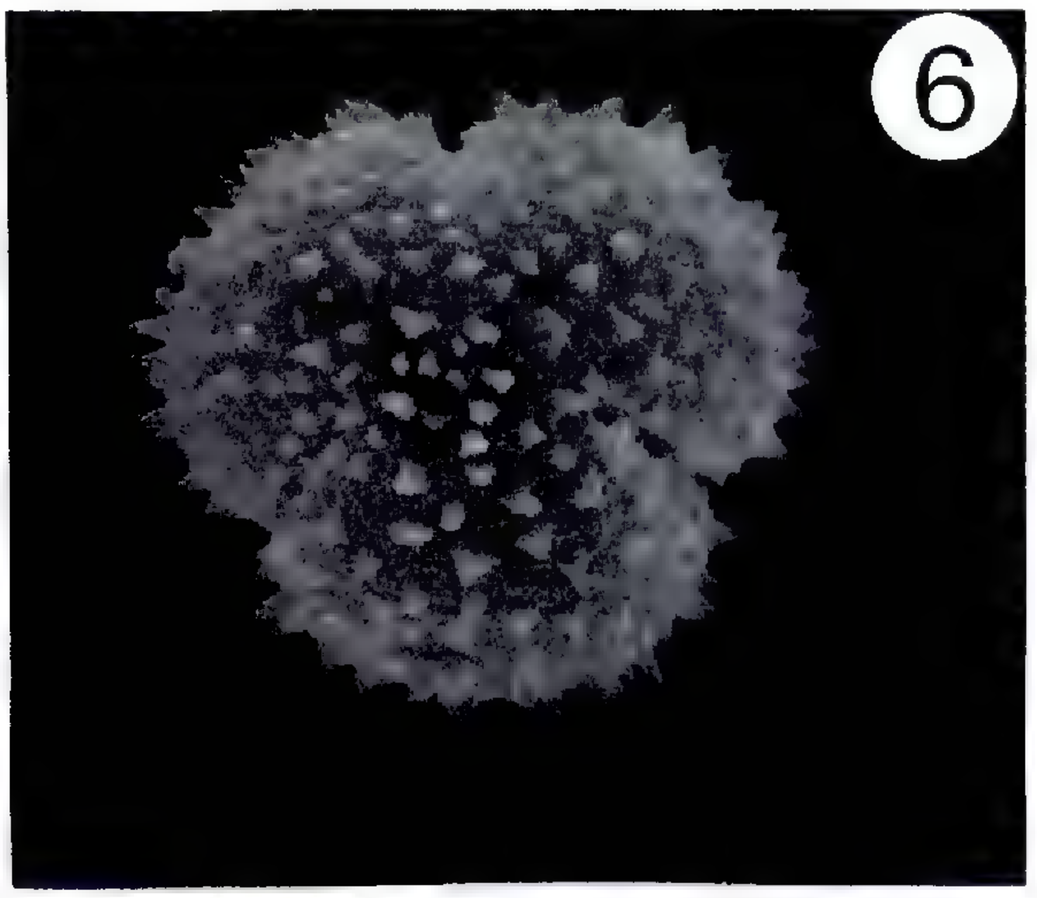
[1]Contributed by Masamichi Takahashi, Biological Institute, Faculty of Education, Kagawa University, Takamatsu-shi 760, Japan.

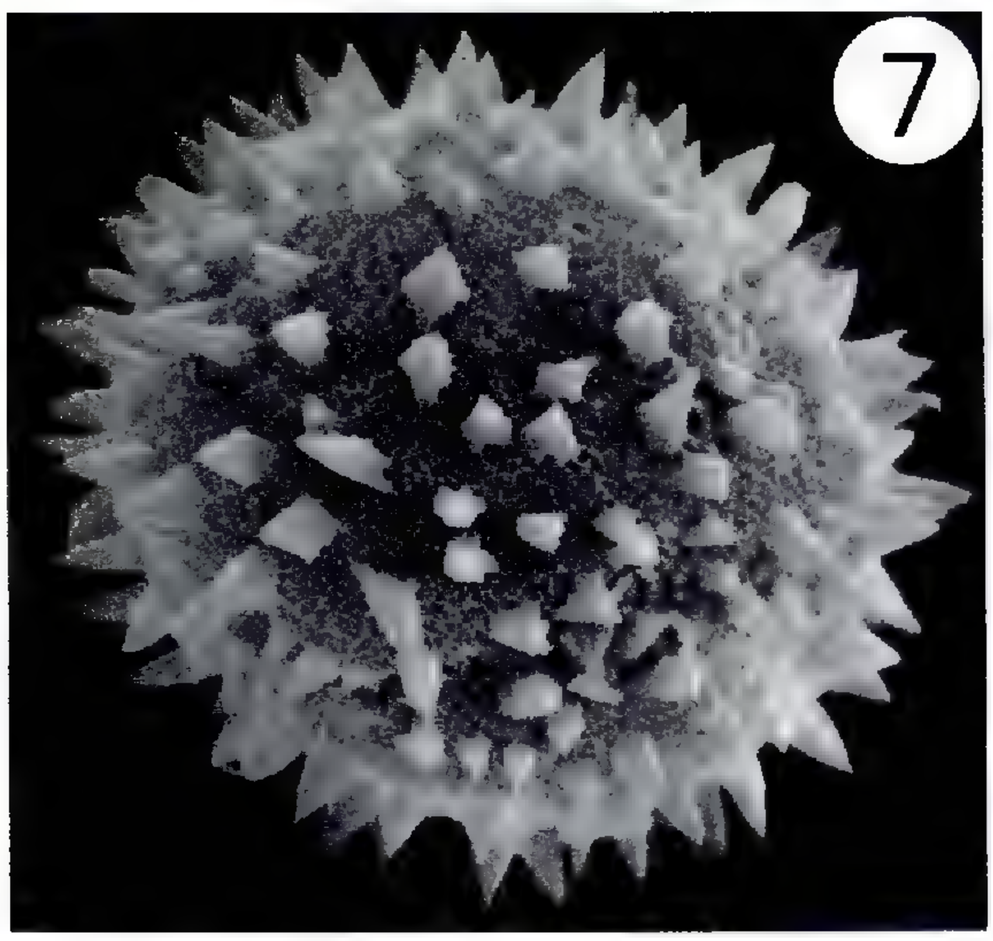
TABLE 2. **Reported chromosome counts for Diphylleia.**

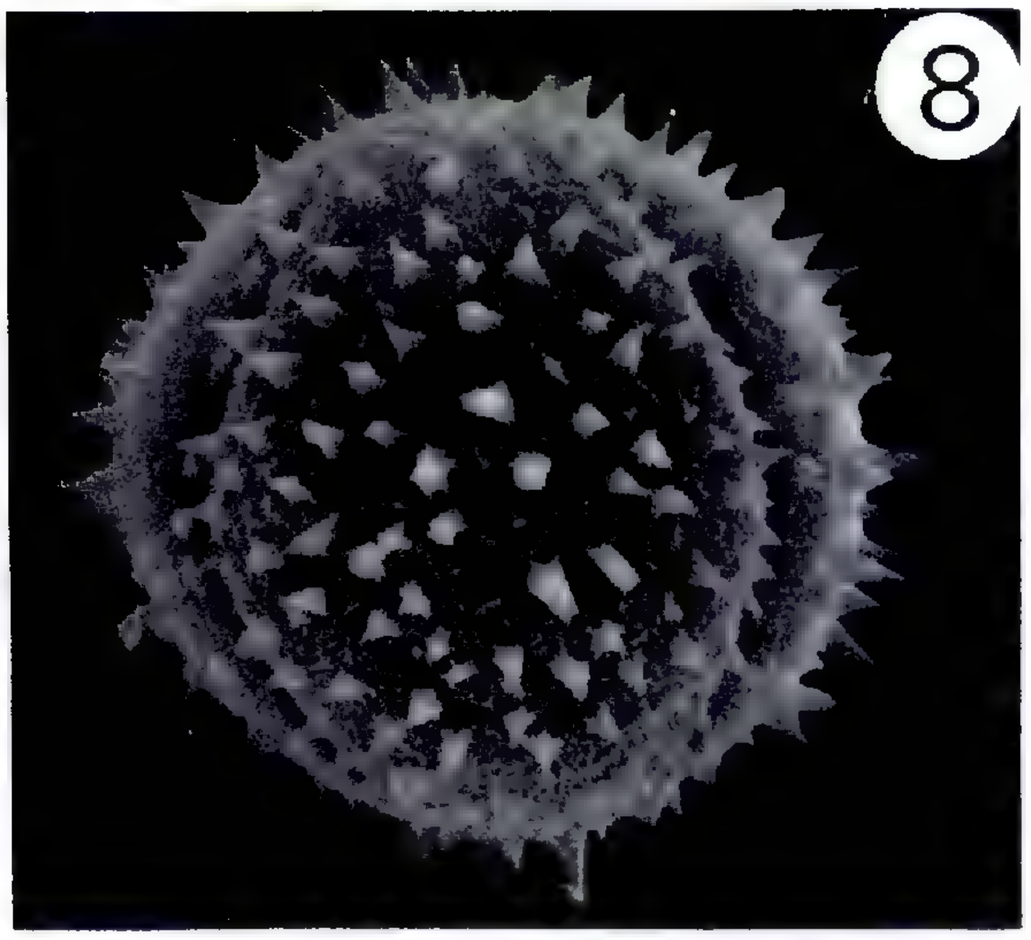
TAXON	CHROMOSOME NUMBER	LOCALITY	REFERENCE	VOUCHER*
D. cymosa	$2n = 12$	U. S. A.†	Langlet, 1928	S
D. grayi	$2n = 12$	Japan, moist forest in mountains of N Japan	Miyagi, 1930	KIEL
	$n = 6$	Japan, Hokkaido, Ishikari Shicho, Mt. Moiwa	Matsuura & Suto, 1935	SAP
	$2n = 12$	Japan, Hokkaido	Soeda, 1942	SAPS
	$2n = 12$	Japan, Honshu, Tochigi Pref., Mt. Shirane	Kurita, 1956	Ehime Univ.
	$2n = 12$	Japan, Honshu, Iwate Pref., Hachimantai	Kuroki, 1967	Ehime Univ.
	$2n = 12$	Japan, Honshu, Hyogo Pref., Hyono-sen	S. Noda & Fujimura, 1970	?
	$2n = 12$	Japan, Honshu, Tochigi Pref., Nikko	Noguchi & Kawano, 1974	Toyama Univ.

* No voucher specimens were cited in any of the reports. If vouchers exist, they are probably in the herbaria indicated.
† See text.









FIGURES 5–8. SEMs of pollen of *Diphylleia*, all × 1400: 5, *D. cymosa* (*J. K. Small s.n.*, 28–29 May 1892), polar view; 6, 8, *D. sinensis* (*Licent 5325*), polar and equatorial views; 7, *D. grayi* (3 July 1952, *A. Kimura & S. Sugaya s.n.*, 3 July 1952), inaperturate.

according to procedures outlined in Erdtman (1960), dehydrated in ethanol, transferred to amyl acetate, and critical-point dried. They were then coated with gold by using an ion sputtering apparatus (Damblon, 1975) and examined with an Akashi MSM-101 scanning electron microscope.

For transmission electron microscopy (TEM) the pollen was fixed in 1 percent osmium tetroxide, dehydrated in an ethanol–propylene oxide series, and embedded in a low-viscosity Epon mixture according to the method of Spurr (1969). Glass knives were used for sectioning on an LKB ultratome. The unstained sections were examined with a Hitachi H-500 transmission electron microscope.

Pollen of *Diphylleia* has been examined by Kumazawa (1936) and Ikuse (1956), who used light microscopy, and by Nowicke and Skvarla (1981), who used light microscopy and scanning and transmission electron microscopy, but none of these authors examined all three species. *Diphylleia* is unique in the Berberidaceae *s.l.* in having spinose pollen grains. Pollen features support other

FIGURES 9–12. Pollen surface ornamentation in *Diphylleia*. 9, TEM, *D. grayi* (*H. Takahashi 366*), section through spine, × 12,000. 10–12, SEMs, all × 3670: 10, *D. cymosa* (*Kologiski & Perino 165*); 11, *D. grayi* (*A. Kimura & S. Sugaya s.n.*, 3 July 1952); 12, *D. sinensis* (*Nan-shui–Bei-diao Team 7164*).

data that indicate a closer relationship between *D. cymosa* and *D. sinensis* than between either of these two and *D. grayi*. In gross morphology, pollen of *D. cymosa* and that of *D. sinensis* are basically the same (FIGURES 5, 6, 8): both are tricolpate or rarely hexarugulate. In contrast, the pollen of *D. grayi* (FIGURE 7) has irregular apertures, which is the same as that reported by Nowicke and Skvarla (1981) in several species of *Berberis* L. and *Mahonia* Nutt. Kumazawa (1936) reported finding some pollen grains of *D. grayi* that had less densely staining spineless, "round areas" containing densely staining "punctations" that he regarded as the germinating pores, while Ikuse (1956) found pollen of *D. grayi* to be polyforate, 34–36 μm in diameter, and with spines 2.5 μm long. In exine ornamentation, however, *D. cymosa* is more similar to *D. grayi* than to *D. sinensis*. The exine of the first two species is characterized by stout spines 1.5–4.5 μm long, while that of *D. sinensis* has slender spines 0.5–2.8 μm long. This difference between *D. cymosa* and *D. sinensis* was also noted by Nowicke and Skvarla (1981). FIGURES 9–12 show exine ornamentation of the pollen of the three species, while TABLE 3 gives pollen size of the samples examined in this study.

TAXONOMIC HISTORY

Diphylleia was first discovered by André Michaux in North Carolina and was described and illustrated in his *Flora Boreali-Americana* (1803). Plants of

TABLE 3. **Pollen size in Diphylleia.***

COLLECTION	POLLEN DIAMETER (μm)	SPINE LENGTH (μm)
D. cymosa		
Kologiski & Perino 165	36.7 ± 2.5 × 32.6 ± 2.7	1.5–4.5
J. K. Small s.n., 28–29 May 1892	32.5 ± 2.5 × 29.7 ± 2.0	1.5–3.7
Radford 5239	35.8 ± 2.4 × 31.1 ± 2.3	1.5–3.8
D. grayi		
Takahashi 366	34.9 ± 2.7 × 31.5 ± 2.2	1.5–4.2
Kimura & Sugaya s.n., 3 July 1952	37.7 ± 1.7 × 33.3 ± 2.2	1.5–4.7
Saito & Kaneko s.n., 18 May 1961	35.0 ± 2.2 × 30.5 ± 2.5	1.4–4
D. sinensis		
Delavay 3862	31.3 ± 2.3 × 30.2 ± 1.7	0.5–2.0
Nan-shui–Bei-diao Team 7164	30.1 ± 2.5 × 28.5 ± 2.6	0.7–2.5
Licent 5325	29.6 ± 2.1 × 28.4 ± 2.0	0.5–2.8

* Thirty pollen grains were measured from each specimen.

Diphylleia from Japan and Sakhalin were probably first collected around 1855 by C. Wright and J. Small; Asa Gray (1859) considered them to be conspecific with the North American *D. cymosa*—an opinion shared by Diels (1900). Schmidt (1868), however, recognizing the plants from Sakhalin to be different from Michaux's *D. cymosa*, described them as *D. grayi*, and Kitamura and Murata (1962) subsequently treated them as a subspecies of *D. cymosa*. Augustine Henry apparently first collected *D. sinensis* in 1888 in what is now the Shennongjia Forest District in northwestern Hubei Province (Henry *in* Thiselton-Dyer, 1889), but he believed the plants he found to be *D. grayi*. Authors subsequent to Henry treated these plants from central China as either *D. cymosa* or *D. grayi* until 1947, when Li described them as *D. sinensis*.

Since the characters that can be used to separate the three taxa are discontinuous, we prefer to treat them as three distinct species.

RELATIONSHIPS AND PLACEMENT OF DIPHYLLEIA

The familial placement of *Diphylleia* has been controversial. Schultz (1832) was the first to place *Diphylleia* in a separate family, the Diphylleiaceae (in which he also placed *Sarracenia*!), while Tischler (1902) proposed that the two genera *Diphylleia* and *Podophyllum* (which included the then-undescribed *Dysosma*) represented the family Podophyllaceae. In this, Tischler has been followed by Hutchinson (1969), Takhtajan (1969), and Airy Shaw (1965), although Hutchinson and Airy Shaw expanded the concept of the Podophyllaceae to include most or all of the herbaceous genera of Berberidaceae. Engler (1903) established a new subfamily in the Berberidaceae, the Podophylloideae, in which he placed *Diphylleia* and all other herbaceous members of the family.

His treatment was followed by Ernst (1964) and Thorne (1968). Cronquist (1968, p. 365) placed the Podophyllaceae (presumably including *Podophyllum* and *Diphylleia*) in his Ranunculaceae but later (1981, p. 126) returned them to the Berberidaceae.

Despite the controversy that exists over the familial placement of *Diphylleia*, there has been little doubt concerning its closest generic relatives. Based on chromosomal, anatomical, and chemical evidence, as well as on overall morphological similarity, *Diphylleia* unquestionably has its greatest affinities with *Podophyllum* and *Dysosma*. Meacham's (1980) study supports this view. However, Nowicke and Skvarla (1981), using palynological evidence, do not feel that these genera are particularly close.

POSSIBILITIES FOR FURTHER STUDIES

Perhaps one of the most interesting studies that could be undertaken with *Diphylleia* would be one dealing with reproductive biology. As far as we have been able to determine, there have been no investigations of this topic. The spinose pollen grains (like those of the Compositae) and the showy clusters of flowers that are held high above the forest floor in early spring strongly suggest insect pollination. However, as in many other herbaceous plants of mixed deciduous forests, the extensive rhizome system also suggests a degree of vegetative reproduction that might account for the large colonies encountered in *D. cymosa* and *D. grayi*. The plants occurring singly or in open colonies in *D. sinensis* possibly indicate a greater dependence on reproduction by seed than by vegetative means, especially since individuals are often found several meters apart. In connection with reproductive biology, it would be of interest to know whether plants are self compatible and, if so, to what extent outcrossing takes place. Study of inter- and intraspecific crosses and knowledge of chromosome behavior in any resultant hybrids are also desirable. Chromosome counts and karyotype analyses of *D. cymosa* and *D. sinensis* would enable comparison with the cytologically well-known *D. grayi*.

Chemical analysis and comparison of the three species could also provide useful information. Except for the above-mentioned work of Murakami and Matsushima (1961), Kimura (1963), and Toyokuni and Toyokuni (1964), we are unaware of any chemical studies involving *Diphylleia*. Comparative flavonoid studies might prove useful, especially in light of the differences among the three taxa revealed by other comparative studies. Comparative evidence from any of the above areas would improve our understanding of the relationships of the three species and could also make possible more detailed comparisons between *Diphylleia* and other genera of the Berberidaceae.

TAXONOMIC TREATMENT

Diphylleia Michaux, Fl. Bor.-Amer. **1:** 203. *pls. 19, 20.* 1803.

Perennial herbs with thickened, creeping rhizomes and coarse, fibrous roots, the rhizomes formed of distinct annual increments, producing stout, 2- (rarely

3-)leaved stem that separates at base in autumn along marked articulation, leaving broad, bowllike excavation on rhizome. Leaves alternate; blade petiolate and peltate (except upper leaf in *Diphylleia grayi,* which is sessile or subsessile and attached at sinus), transversely oblong to reniform-orbicular, 2-cleft with divisions shallowly to coarsely lobed and prominently dentate, palmately veined with main veins connected by secondary, reticulate veins, pubescent or sparsely pubescent with unicellular hairs. Inflorescence a terminal, pedunculate (peduncle rarely branched below), usually many-flowered cyme or umbel, the branches glabrous or pubescent. Flowers pedicellate, actinomorphic, 3-merous; sepals 6 in 2 (rarely 3) whorls, white or pale green, deciduous prior to or just at anthesis; petals 6 in 2 whorls, white; stamens 6, antipetalous, the anthers basifixed, longitudinally dehiscent, the thecae separating from connective and ultimately attached only at apex, the pollen conspicuously spiny; ovary superior, ellipsoid, unilocular, the style absent or very short and thickened, the stigma peltate, cristate, the placentation parietal near base of ovary, the ovules 2 to 11, anatropous. Fruit a globular or broadly ellipsoid berry, dark blue, glaucous, to 1 cm broad, borne on thickened, disclike, lobed receptacle. Seeds oblong to ovoid, rounded on all sides or flattened to concave ventrally, straight or slightly curved, surface minutely rippled and microscopically striate. Embryo straight or slightly curved, ca. 2–4 mm long, with 2 cotyledons, embedded in endosperm. Chromosome number: $n = 6$.

TYPE SPECIES. *Diphylleia cymosa* Michaux.

A genus of three species, with one in each of three widely disjunct areas: the southern Appalachian Mountains of the southeastern United States; central and northern Japan, Sakhalin, and the southern Kuril Islands (Kunashiri Island); and central and southwestern China.

KEY TO THE SPECIES OF DIPHYLLEIA

1. Inflorescence glabrous; ovules 2 to 4; leaves glabrous or sparsely pubescent. ..... 1. *D. cymosa.*
1. Inflorescence pubescent; ovules 5 to 11; leaves pubescent.
   2. Upper leaf distinctly petiolate, the petiole more than 2.5 cm long; petals less than 9 mm long and 6 mm wide; flowers usually 15 or more. ..... 2. *D. sinensis.*
   2. Upper leaf sessile or with petiole less than 1 cm long; petals more than 8 mm long and 6 mm wide; flowers usually 12 or fewer. ..... 3. *D. grayi.*

1. **Diphylleia cymosa** Michaux, Fl. Bor.-Amer. **1:** 203. 1803. FIGURE 13.

Plants 4–12 dm tall, growing in dense or loose colonies, occasionally as scattered individuals. Petiole 7–22 cm long in lower leaf, 3–15 cm long in upper; blade peltate, suborbicular, reniform or transversely oblong, deeply cleft at apex and base, 14–30 by 19–47 cm in lower leaf and 9.5–33 by 13–42 cm in upper, deeply cut to lobed at margin and coarsely doubly serrate, sparsely pubescent along main veins beneath or glabrescent, usually glabrous above or with few hairs along main veins. Peduncle solitary, occasionally bifurcate, 0.6–3.3 cm long, glabrous; inflorescence 7.5–41 cm long including peduncle, 3.7–

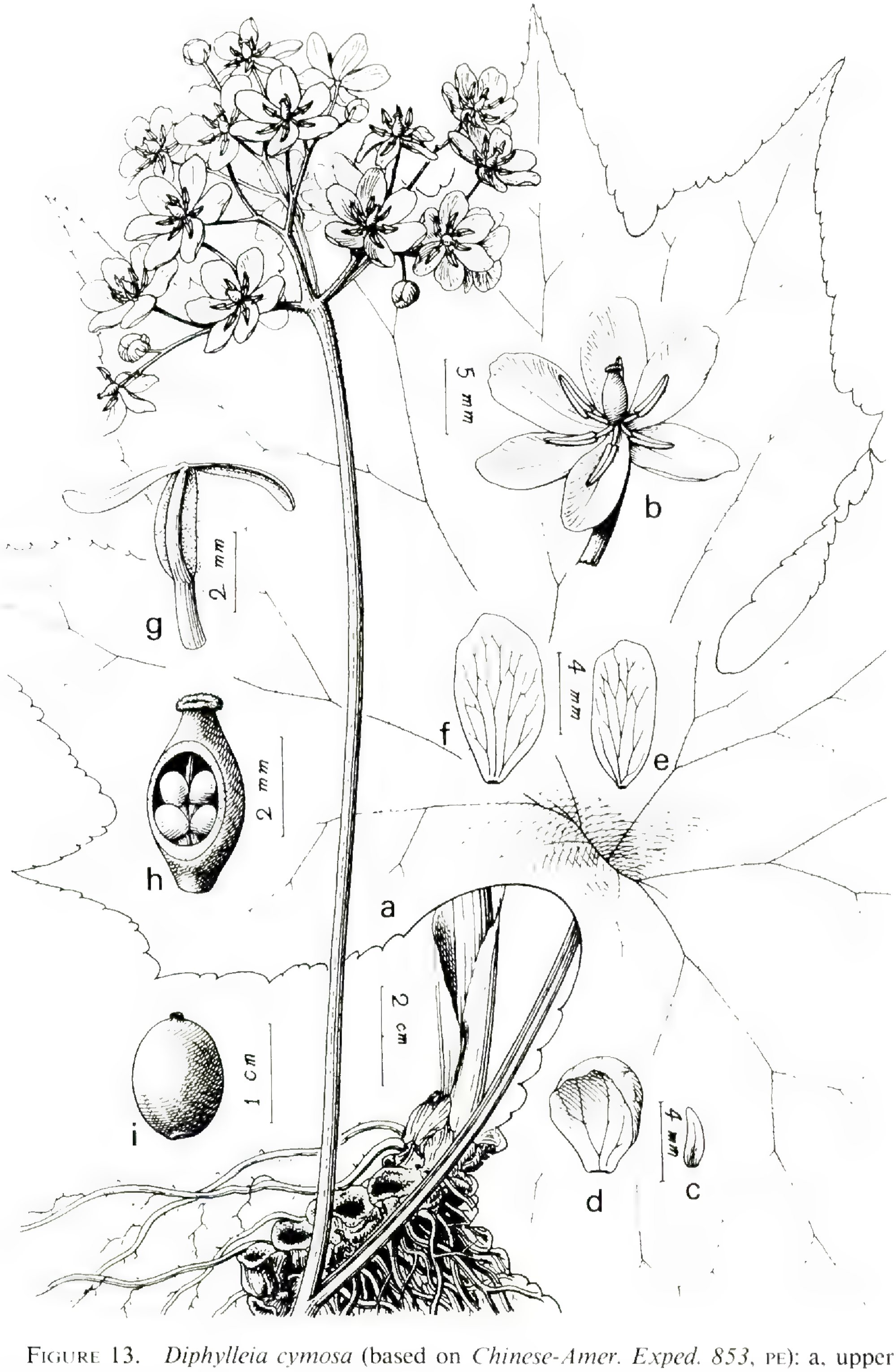


FIGURE 13. *Diphylleia cymosa* (based on *Chinese-Amer. Exped. 853*, PE): a, upper leaf, inflorescence, rhizome, roots; b, flower; c, outer sepal; d, inner sepal; e, outer petal; f, inner petal; g, stamen; h, ovary; i, fruit.

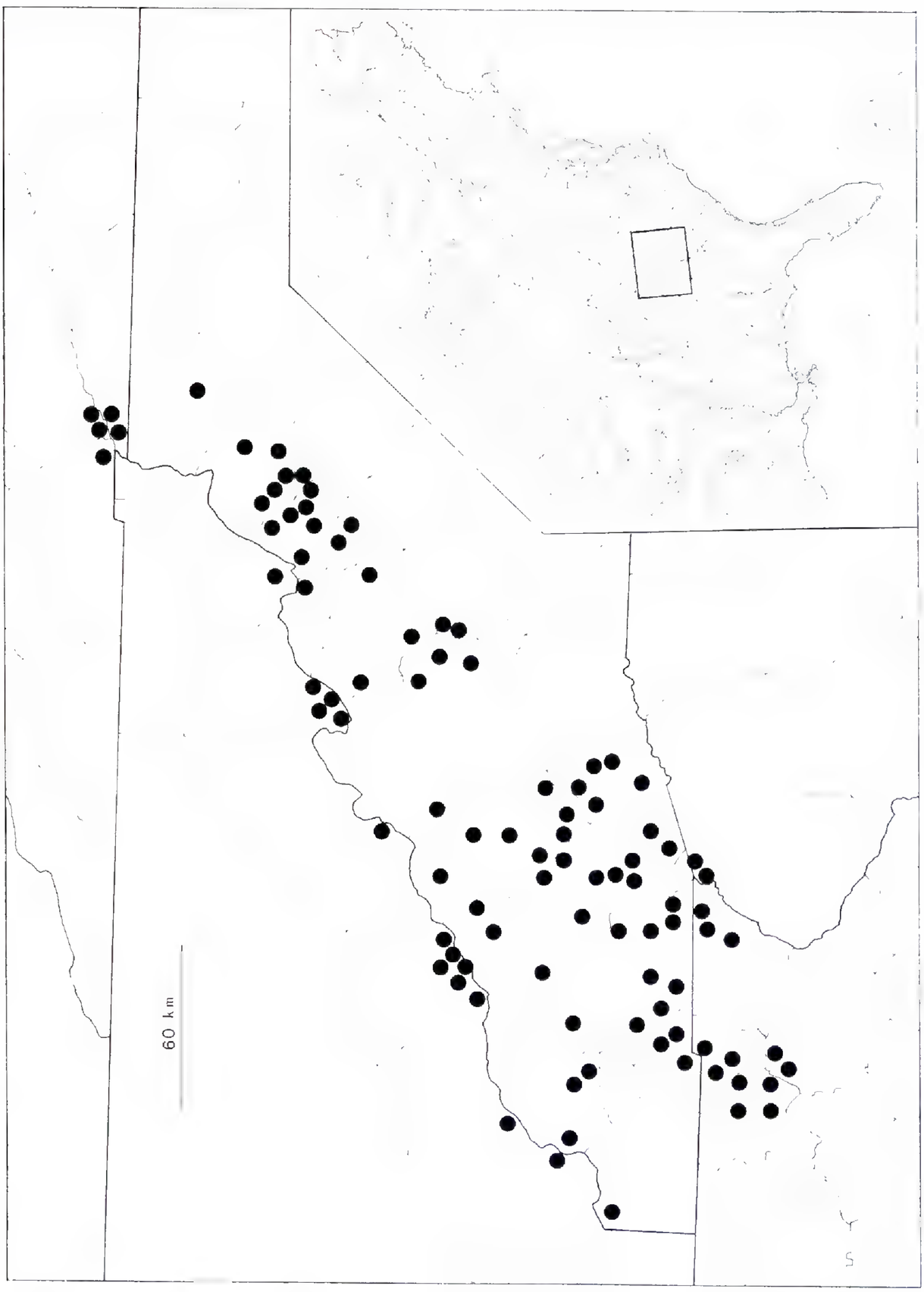
14 cm wide, glabrous (rarely with few scattered hairs when young). Flowers (6 to) 14 to 70 or more; pedicels 0.8–4 cm long; outer sepals lanceolate, oblanceolate to spatulate, or reduced and scalelike, ca. 1.7–4.5 by 0.4 mm; inner sepals obovate to suborbicular, 2.5–6 by 3.5–4 mm; outer petals narrowly obovate, 9–11 by 4.5–6 mm; inner petals elliptic-obovate to obovate, 10–13 by 6–7 mm; stamens 3.6–4.5 mm long, filaments 1–2 mm long, anthers ca. 2 by 1.2 mm; ovary ellipsoid, 3.5–5 by 2–2.5 mm, style ca. 0.3 mm long, stigma ca. 0.5 by 1 mm. Berry globular to very broadly ellipsoid, 0.5–1.2 cm broad, blue, glaucous, on pedicel 1–3.8 cm long. Seeds 2 to 4, ± oblong, 3.9–7 by 2–4.7 mm, rounded dorsally, flattened to concave ventrally. Chromosome number: $n = 6$ (but see under cytology above).

TYPE. United States, mountains of North Carolina, 1786?, *A. Michaux s.n.* (lectotype, P, photo A; isolectotype, P).

DISTRIBUTION AND ECOLOGY. Moist places in mixed deciduous and coniferous forests, often along seepages and small streams, 1000–1650 m alt. United States: southwestern Virginia, western North Carolina, and eastern Tennessee to northeastern Georgia and extreme northwestern Oconee County, South Carolina; restricted to Blue Ridge of southern Appalachian Mountains. (MAP 1.)

SPECIMENS EXAMINED. **United States.** GEORGIA. Rabun Co.: Rabun Bald, 34°57′N, 83°18′W, *Boufford & E. W. Wood 17033* (NCU); along Darnell's Creek SE of Dillard, *Duncan & McDowell 10852* (GA); 2 mi N of Clayton, *Pyron & McVaugh 847* (GA). Towns Co.: N-facing slope, Hogpen Gap, Richard Russell Scenic Hwy., *Coile 346* (NCU); N-facing ravine just N of summit of Hightower Bald, *Duncan 7597* (GA). Union Co.: 3 mi W of Vogel State Park, *Hardin 259* (GA); Brasstown Bald, *Howell 407* (US); Sosbee Cove, above Vogel State Park, *Kral 59676* (VDB); 1.5 mi from top of Brasstown Bald, *Lord 364* (NCU); cove E of Wolfpen Gap, *Pyron & Duncan 46* (GA); Blairsville, Lock Gap, *I. Stuckey s.n.* (VDB). White Co.: 2.5 map mi above jct. of Chattahoochee R. and Spoibine Creek, *Duncan & Hardin 16361* (GA); Hogpen Gap, off hwy. 348, *Wohlers 122* (GA). NORTH CAROLINA. "Mountains of North Carolina," *A. Michaux s.n.*, 1786? (Michaux herb. at P, IDC 6211. 47: I. 2, 3). Iron Mt., *Canby s.n.*, Sept. 1876 (NY). Ashe Co.: Bluff Mt., *Radford 44012* (NCU). Avery Co.: 1.2 mi SSW of Minneapolis on U.S. 19E, *Ahles & Ashworth 39451* (NCU); NNW of Linville, 1 mi SSW of jct. N.C. 184 and 105 on 105, *Ahles & Duke 43632* (NCU); Grandfather Mt., *Blomquist 3681* (DUKE), *Heller s.n.*, 22 July 1890 (LE, NY), *Mohr s.n.*, 28 July 1894 (US), *Mullen 81* (NCSC), *Seymour 91 8 13* (DUKE); ca. 7 mi ENE of Linville along U.S. route 221, *McVaugh 8937* (GA, NCU, VDB); 2 mi E of Linville along U.S. route 221, *Robertson & Umber s.n.*, 3 June 1973 (GH); vic. of Banner Elk, *Steele 18* (US); Linville Falls, *Weiss s.n.*, 30 May 1959 (VPI); NE of Linville, 3 km E of U.S. route 221 on county road 1514 (Edgemont Road), *E. W. Wood & Boufford 4150a* (BM, CM, KYO). Buncombe Co.: Craggy Mt., *Biltmore Herb. 1213*[b] (BM, GH, L, NCU, NY, US, W); Pisgah Natl. Forest, ca. 10 mi SE of Dillingham, *Boufford et al. 14417* (NCU); S flank Black Mt., *N. L. & Mrs. Britton s.n.*, 18 Sept. 1885 (NY); Black Mt., *Canby s.n.*, June 1868 (NY); Blue Ridge Pkwy. at Craggy Gardens, *Freeman 58196* (NY); wet woods in Craggy Gardens, *Hicks & Bartley 2248* (GH); Black Mts., *LeRoy s.n.* (NY), *Rugel 243* (BM); Graybeard Mt., *Pollard s.n.*, 16 May 1901 (US); Craggy Mts., *Rydberg 9446* (LE, NY). Burke Co.: near Linville, *Barkley & Hicks 2031* (NY, US). Caldwell Co.: NW corner of Caldwell Co. on U.S. 221, hwy. to Grandfather Mt., *Radford & Stewart 1575* (NCU). Cherokee Co.: 2.3 mi E of Tennessee state line on Tellico R. Road, *Pittillo & Floyd 5710* (WCUH). Clay Co.: near Perry Gap, ravine at end of U.S. Forest Service Road along Buck Creek (N of U.S. route 64), *Boufford et al. 14165* (NCU), *17001* (BM); ca. 15 mi E of

Haysville, Chunky Gal by U.S. route 64, *Kral 60290* (VDB); Chunky Gal Mt., W of Rainbow Springs on U.S. 64, *Pittillo et al. 4289* (WCUH); Buck Creek near U.S. 64, 2 mi SW of Clay-Macon Co. line, *Radford 12162* (NCU); Perry Gap Road above Buck Creek, 4 mi N of U.S. 64, *Fox & Godfrey 5056* (NCSC). Graham Co.: 5.1 mi N of jct. of Cherokee Co. roads 1391 and 1399 on U.S. Forest Service Road 423, *Boufford et al. 14518* (NCU); 4 mi E of Fontana, *Radford 11870* (NCU, VDB); 4 mi S of Robbinsville, *Radford 14196* (NCU); Joyce Kilmer Mem. Forest, *Tucker & Pittillo 141* (WCUH). Haywood Co.: Junaluska Mt., *Batchelder 5081, 5082* (GH); Junaluska Mt., Lake Junaluska, *Blomquist 3682* (DUKE); ca. 1.6 mi S of Sunburst on N.C. 215 along West Fork Pigeon R., *Boufford et al. 15041* (NCU); Mt. Sterling, *Caughey 716* (NCSC); Bill Camp Cove, *Couch s.n.*, 24 July 1926 (NCU); Jonathan Creek, *Pyron 63* (GA); Eagles Nest, *Ruth 367* (GH); Blue Ridge Pkwy. at Frying Pan Gap, *Smathers s.n.*, 25 June 1958, 22 June 1959 (WCUH); Balsam Mt., *J. D. Smith s.n.*, 11 Aug. 1882 (US); near Waynesville, Eagles Nest, *Standley 5459* (US); county road 1334 2.8 mi N of intersection with county road 1335, *Wyatt 267* (DUKE); Crabtree Bald, county road 1505 ca. 5 mi NE of intersection with N.C. route 209, *Wyatt et al. 598* (DUKE). Jackson Co.: 14.7 mi NW of N.C. route 215 on Blue Ridge Pkwy., *Boufford et al. 13529* (NCU); Balsam, *Braun s.n.*, 14 July 1911 (US); 5.2 mi S of Dillsboro on county road 1371, *Bryson 47* (WCUH); Tuckaseegee R., ½ way from Sylva to Cashiers, *Coker s.n.*, 21 Aug. 1939 (NCU); 10 mi S of Cullowhee P.O. on N.C. 107, *Crisp s.n.*, 29 June 1965 (WCUH); E of Glenville, Slatten Creek, *Godfrey & O'Connell 51951* (DUKE, NCSC); Soco Falls, *Hendrix B-22* (DUKE); 14 mi SSE of Cullowhee P.O. on N.C. route 107, *Hoffman 70* (WCUH); Mull Creek, *Murtagh 230* (WCUH); Nantahala Natl. Forest, N.C. route 107 at pipeline from Lake Thorpe, *Pittillo 2876* (E, FARM, GA, GH, NCU, NY, VDB, WCUH); Rough Butt Bald Mt., *Ramseur 389* (NCU); Wet Camp Gap, *W. B. & M. B. Schofield 8527* (DUKE); ca. 4 mi S of Thorpe Power Sta. on N.C. route 107, *Sharpe 26* (WCUH); above Glenville Power Plant, *B. Smith s.n.*, 10 May 1953 (WCUH); 15.1 mi S of Cullowhee P.O. on N.C. route 107, *Taylor 38* (WCUH). Macon Co.: Satulah, *L. B. s.n.*, 24 May 1934 (NCU); near Highlands, *Biltmore Herb. 1213* (GH, IF, NY, P, US, W), *1213c* (FI, G); under Dry Falls, *Coker & party s.n.*, 28 Aug. 1932 (NCU); near Rainbow Springs, *D. S. Correll 3522* (DUKE); 4.5 mi W of Fish Checking Sta. on Nantahala Forest Road, *Fox & Godfrey 3081* (NCSC); U.S. route 64 at Glade Gap, *Freeman 59143* (NCU); Highlands, *Gibbes s.n.*, July 1882 (NY), *Harbison s.n.*, 13 July 1901 (GH); county road 1678 2.2 mi from jct. with county road 1679, *Metheney 076* (WCUH); Cullasaja R. at Dry Falls, *Oosting 34427* (DUKE); Highlands, *Palmer 42502* (NY); county road 1001 S of Cullowhee Gap to Wildcat Road, E to Bryson Branch, *Pittillo 4050* (WCUH); 13 mi N of U.S. route 64 on Rainbow Springs–Aquone Forestry Road, *Radford 5239* (NCU); 4 mi N of Highlands, Cole Mt. Road, *Radford 6123* (NCU); Cullasaja Gorge, High Falls, *W. B. Schofield 8776* (DUKE); Crow Creek ca. 0.5 mi below Cullasaja Falls, *Stewart & Hechenbleikner s.n.*, 25 July 1938 (NCU); Stewart Trail between Bearpen and Albert Mt., *Stewart & Hechenbleikner s.n.*, 12 Aug. 1938 (NCU). Madison Co.: 0.2 mi N of Betsy Gap and Haywood Co. line on N.C. 209, *Bozeman et al. 9102* (GA, GH, NCU, NY, VDB). McDowell Co.: near Big Craggy on Blue Ridge Pkwy., *Ahles & Bell 17697* (NCU); Blue Ridge, *W. F. s.n.*, 1872 (GH). Mitchell Co.: Roan Mt., *Canby s.n.*, June 1868, June 1879 (NY), *Chickering s.n.* (US), *J. D. Smith s.n.*, 15 Sept. 1884 (GH, US), *Shallert s.n.*, 1927 (DUKE); Spruce Pine, *Hyams s.n.*, June 1878 (US); Little Roan, *Merriam s.n.*, 1 Sept. 1892 (US). Swain Co.: Great Smoky Mts. Natl. Park, Round Bottom Road from Heitooga Overlook, *Athey s.n.*, 16 May 1973 (VDB); 3.4 mi from N.C. hwy. 28 on Mica Knob Road, *Bell 3117* (NCU); Nantahala Gorge, 3 mi SE of Beechertown, *Radford et al. 8021* (NCU); Great Smoky Mts. Natl. Park, Smokemont, foot of Hughes Ridge, *Jennison 445* (GSMNP, TENN); Great Smoky Mts. Natl. Park, upper Chasteen Creek, *Jennison & J. G. Smith 2291* (GSMNP, TENN); Brookside, Rich Mt., *Hunnewell 10337* (GH). Transylvania Co.: Whitewater R. near jct. with Bohaynee Road bridge, *Bannister & Anderson 432* (NCU); near head of Davidson R. near Fish Rearing Sta., Pisgah Ranger Distr., *Beaman 50026* (NCSC); 2.7 mi N of N.C. 215 on Courthouse Creek Road (U.S. Forest Service



MAP 1. Distribution of *Diphylleia cymosa* in the United States.

Road 140), *Boufford & E. W. Wood 16283* (NCU); W Fork French Broad R., jct. U.S. 64 near Rosman, *Bozeman et al. 9122* (BM, TENN); on trail, Black Rock to Sapphire, *Coker s.n.*, 18 Aug. 1910 (NCU); Blue Ridge Pkwy. between Wagon Road Gap and Beech Gap, *Freeman 57326* (NCU); Pink Beds, *House 4008* (GH); road from Mt. Pisgah to Brevard, *Oosting 34686* (DUKE); Pisgah Ridge, U.S. route 276 1.8 mi below jct. with Blue Ridge Pkwy., *Roberts & Keil 7416* (VDB); Sapphire, NE-facing cove on Hogback Mt., *Ware & White 3055* (NCU, VDB). Watauga Co.: 1.2 mi E of Bamboo on road to Triplett, *Ahles & Ashworth 39619* (NCU); Blowing Rock, *H. L. B. 3680* (DUKE); Rich Mt. NW of Boone, N-facing cove near lookout tower, *Boufford & E. W. Wood 16310* (WCUH), *Chinese-Amer. Bot. Exped. 853* (KUN, NAS, PE, WH); Linville Road, *Churchill s.n.*, 1899 (TENN); along Long Hope Creek on W slope of Old Field Bald, *Hardin 13255* (NCSC); upper end of Long Hope Creek, *Hardin 13273* (NCSC); Potato Hill, N of jct. of state roads 1324 and 1306, *Kologiski & Perino 165* (GH, NCSC); 2.5 mi SE of Aho, *Radford 11111* (NCU); Rich Mt., *Radford 45373* (NCU, USCH); NW slope of Hanging Rock Ridge, *Rohrer 1790* (NCU); Grandfather Mt., *Seymour 91 8 13* (GH); 5 mi W of Blowing Rock, *J. K. Small & Heller s.n.*, 1891 (G, GH). Yancey Co.: 3.4 mi NW of Swiss, *Ahles & Duke 50705* (GH); Mt. Mitchell, *Palmer 42540* (GH), *Rhoades s.n.*, 1932 (GH), *Shallert s.n.*, 1923 (DUKE). SOUTH CAROLINA. Oconee Co.: near S.C. route 107 near North Carolina line, *Batson & Swails s.n.*, 1956 (SCUH); Ellicott Wilderness Area of Sumter Natl. Forest. E fork of Chatooga R., *Kirkman & Ellis 1201* (GA). TENNESSEE. Doe R. Valley, *Ball s.n.*, Sept. 1884 (US). Blount Co.: Great Smoky Mts. Natl. Park, trail to Gregory's, *Cain s.n.*, 3 Aug. 1929 (TENN). Carter Co.: Roan Mt., 1 mi below Cold Spring, *D. M. Brown 27* (DUKE); Roan Mt., below Carver's Gap, *Cannon 146* (NY, US); along old hacktrail leading to summit of Roan Mt., *Wofford 81-36* (TENN). Cocke Co.: near Lemon's Gap, *Kearney 610* (NCU, NY, US). Greene Co.: near summit of Cold Spring Knob, *Sharp & D. K. Smith s.n.*, 23 Sept. 1973 (TENN). Monroe Co.: Cherokee Natl. Forest, Citico Creek WSA, Falls Branch Scenic Area, *Malter 53107* (TENN); Cherokee Natl. Forest, near Beech Gap, *Sharp 715* (TENN). Sevier Co.: Great Smoky Mts. Natl. Park, Newfound Gap along U.S. route 441, *Boom 39435* (L); Great Smoky Mts., "Spruce Flat," Roaring Fork, *Braun s.n.*, 25 April 1927 (US); Chimney Caps, *Cain s.n.*, 12 June 1933 (TENN); Greenbrier, Lester Prong, *Cain & Duncan 401:2* (TENN); Great Smoky Mts. Natl. Park, Chimney Caps Trail, *Duncan 406* (GA); Lester Prong, *Duncan 901* (NCU); Great Smoky Mts. Natl. Park, 1 mi E of Seilers Bald, *Fosberg 18718* (NCSC); Mt. LeConte, *Iltis 1355* (NCSC); Smoky Mts., Balsam Point, *Hunnewell 14997* (GH); Little Pigeon R., *Hunnewell 14178* (GH); W fork of Little Pigeon R., ca. 1 mi W of Chimneys Campground, *Hyypio 453* (VDB); Great Smoky Mts., Greenbrier, near Ramsey Prong Creek, *Jennison 39* (GSMNP, TENN); near Jakes Gap, *Jennison 2828* (GSMNP); trail up Mt. LeConte, *T. Jones s.n.*, 4 May 1935 (TENN); Mt. LeConte, *Ramseur 1662* (NCU), *Underwood 2669* (TENN); Double Springs Gap, *W. B. Schofield 10038* (DUKE); Mt. LeConte, Roaring Fork, *Sharp 640* (TENN); Great Smoky Mts., Elkmont, *Whmeyer 350* (GA). Unicoi Co.: E side of Rich Mt., valley of Higgins Creek, *E. H. Cooley et al. 8855* (TENN); Big Bald Mt., *James s.n.*, 5 Sept. 1955 (TENN); along U.S. route 23, Flag Pond, *James 16579* (TENN); Unaka Mt. near Beauty Spot, *Price 702* (DUKE); near Bald Mt., *Price 756* (USCH). VIRGINIA. Grayson Co.: Pine Mt., Solomon Branch, *Sheffey s.n.*, 18 May 1974 (FARM); White Top Mt., *Britton et al. s.n.*, 1892 (G, NY), *Roller s.n.*, 1939 (VPI), *Sharp 20496* (TENN), *Stevens & Harvill 25604* (FARM), *Uttal 11182* (VPI); Mt. Rogers, *Massey s.n.*, 1946 (VPI), *Nicely 826* (VPI), *Reedy 65-4* (EHCV), *C. E. Wood, Jr., 1403* (GH, VPI). Smyth Co.: White Top Mt., *Camp 1564* (NY), *Core (Moldenke) 6846* (NY), *J. K. Small s.n.*, 28–29 May 1892 (GH, US), *Stevens & Harvill 25656* (FARM); Mt. Rogers, *Kral 11684* (NCU, VDB). Washington Co.: Taylor's Valley, *Jervis s.n.*, 9 Aug. 1967 (EHCV).

In addition to the two sheets of *Diphylleia cymosa* in the Michaux Herbarium at P (IDC 6211. 47: I. 2, 3), there are also two sheets in the general herbarium at P that are most likely part of the original collection and represent type

material. Both of the latter sheets are annotated "Herb. Richard," and both also bear labels with "Herbarium Drake." Background information on the role of L. C. Richard in the authorship of *Flora Boreali-Americana* and on the history of the Richard and Drake herbaria support this contention, as outlined below.

Gray (1882a, p. 183), commenting on specimens in the "older herbaria," said of Michaux's *Flora Boreali-Americana* (1803), "It is known through tradition that this work was prepared by L. C. Richard, from the collections of the elder Michaux; but he wholly withheld his name, which therefore cannot be cited." Gray (1882b) also mentioned that Richard's herbarium contained an almost complete set of the plants described in that work. Previous to Gray, Hooker (1842, p. 432) had written that "Richard is the anonymous author of the *Flora Boreali-Americana* of Michaux, in 2 vols. 1803." It is of interest to note that Fedchenko (1937), in his treatment of the Berberidaceae for *Flora SSSR*, cited the authorship of *Diphylleia* as "L. C. Richard in A. Michaux."

Louis Claude Richard's son, Achille Richard, continued his father's botanical work and inherited his father's herbarium (Gray, 1882b). The Richard herbarium later came into the hands of De Franqueville (Roze, 1891) and was eventually obtained by Drake del Castillo, who, according to Bureau (1904), acquired many of the larger private herbaria in Europe during the latter part of the 1800's. In summarizing the contents of the Drake herbarium, Bureau mentioned that A. Michaux's collections from North America were among them. Stafleu and Cowan (1976, p. 872) also mentioned the fact that the herbaria of L. C. and A. Richard are now at P through the De Franqueville and Drake herbaria. It appears obvious that the two specimens at P that are annotated "Herbarium Richard" are part of Michaux's original collections of *Diphylleia* from North America and were among the material available to L. C. Richard when he prepared *Flora Boreali-Americana*. These two sheets, in addition to the two in the Michaux Herbarium, must therefore be considered in the designation of a lectotype.

The protologue of *Diphylleia cymosa* Michaux includes a description of all above-ground parts of the plant plus two plates (*tt. 19, 20*). One plate (*t. 19*) illustrates the habit of a plant in fruit (including a rhizome that more closely resembles that of *Podophyllum peltatum* L.); the other shows only the upper portion of a stem with the upper leaf and the inflorescence. Neither illustration exactly matches any of the four sheets of original material, although one sheet in the Michaux Herbarium (IDC 6211. 47: I. 2) and one in the general herbarium at P are quite similar to the illustration in *t. 20* of *Flora Boreali-Americana*. The Michaux Herbarium specimen, however, is in fruit (as is IDC 6211. 47: I. 3), while each of the two sheets in the general herbarium at P has both flowers and fruits. One of these sheets is labeled (in Michaux's handwriting?) with essentially the same information as in the original description. The characteristics of the attached specimens agree with the original description in *Flora Boreali-Americana*, and we designate the flowering material on this sheet as the lectotype of *D. cymosa* Michaux.

Although the three species of *Diphylleia* are remarkably alike, *D. cymosa* appears to be most similar in overall morphological features to *D. sinensis*, of

central and southwestern China. Both have a petiolate, peltate upper leaf, smaller flowers, more abundantly flowered inflorescences, and tricolpate or hexarugulate pollen—characters not found in *D. grayi*, of Japan. The inflorescences are commonly cymose in *D. cymosa* and *D. sinensis* but are frequently umbellate in *D. grayi*. However, *D. sinensis* and *D. grayi* are similar in the pubescent inflorescence, the greater number of ovules per ovary, and the exine ornamentation of the pollen. It is difficult, if not impossible, to say with certainty which species is most primitive.

2. **Diphylleia sinensis** H. L. Li, J. Arnold Arbor. **28:** 442. 1947. FIGURE 14.

Diphylleia cymosa Michaux subsp. *sinensis* (H. L. Li) T. Shimizu, Hikobia Suppl. **1:** 450. 1981.

Plants 4–10 dm tall, growing in dense to loose colonies or individually. Petiole of lower leaf 7–20 cm long, of upper (2.5–)6–13 cm long; blade peltate, reniform or reniform-orbicular to transversely oblong, 19–40 by 20–46 cm in lower leaf and 6.5–31 by 19–42 cm in upper, 2-cleft with divisions undulate or shallowly 3- to 6-lobed, margin irregularly dentate with teeth apiculate, pubescent with whitish hairs beneath, sparsely so or subglabrous above. Peduncle 3.5–28 cm long, solitary, occasionally bifurcate; inflorescence 4.2–35 cm long including peduncle, 3.5–10 cm broad, branches pubescent or glabrescent in fruit. Flowers (8 to) 15 to 51; pedicels 0.4–3.7 cm long; outer sepals lanceolate to linear-lanceolate, 2.3–3.5 by 0.7–1.2 mm; inner sepals very broadly elliptic to subcircular, 4–4.5 by 3.8–4 mm; outer petals narrowly to broadly obovate, 5–8 by 2.5–5 mm; inner petals narrowly elliptic to narrowly obovate, 5.5–8 by 2.5–3.5 mm; stamens ca. 4 mm long, laminar filaments 1.7–2 mm long, anthers ca. 2 by 0.6 mm; ovary ellipsoid, 3–4 by 1.8–2 mm, ovules 5 to 11, style absent or represented by slight constriction at summit of ovary, stigma ca. 0.3 by 1 mm. Berry globular to broadly ellipsoid, 10–15 by 6–10 mm broad, dark blue or purple-black, on pedicel 1–3 cm long. Seeds 2 or 3, ovoid, ca. 5.5 by 3.5 mm, ± rounded on all sides or only slightly flattened ventrally. Chromosome number: unknown.

TYPE. China, western Sichuan Province, July & August 1908, *E. H. Wilson 814* (lectotype, GH (the fruiting element); isolectotype, US).

DISTRIBUTION AND ECOLOGY. Moist deciduous and coniferous forests, sometimes bamboo thickets, 1880–3700 m alt. China: western Hubei, southern Shaanxi, southern Gansu, Sichuan, and northwestern Yunnan. (MAP 2.)

SPECIMENS EXAMINED. **China.** GANSU: Zhouchu Xian, *P. Z. Guo 5148, 5561* (WUK), *S. Zhang 00406* (PE), *W. J. Zhou 294* (NWTC); Zhang Xian, *Y. S. Lian 790160* (NWTC); Dang Chang Xian, *Y. S. Lian 790971* (NWTC); Die Bu Xian, *Y. S. Lian 800328* (NWTC), *C. R. Wang 15643* (WNC); Liou h'ia tien ze, col du Koan Chan, *E. Licent 5325* (BM, K, P), *5335* (K), *5336* (K); Tianshui Xian, *J. M. Liu 10182* (PE), *Z. W. Zhang 151* (WUK); Ming Xian, *J. C. Wang 200* (NWTC), *Xu-Mo-Tin Team 387* (WNC); Longde Xian, *Z. P. Wang 13120* (WUK); Xigu Xian, *Z. P. Wang 15159* (PE, WUK); Jing Yuan, *Z. P. Wang 17074* (PE); Wu Shan Xian, *without collector 324* (NWTC). HUBEI: Badong Xian, *F. H.*

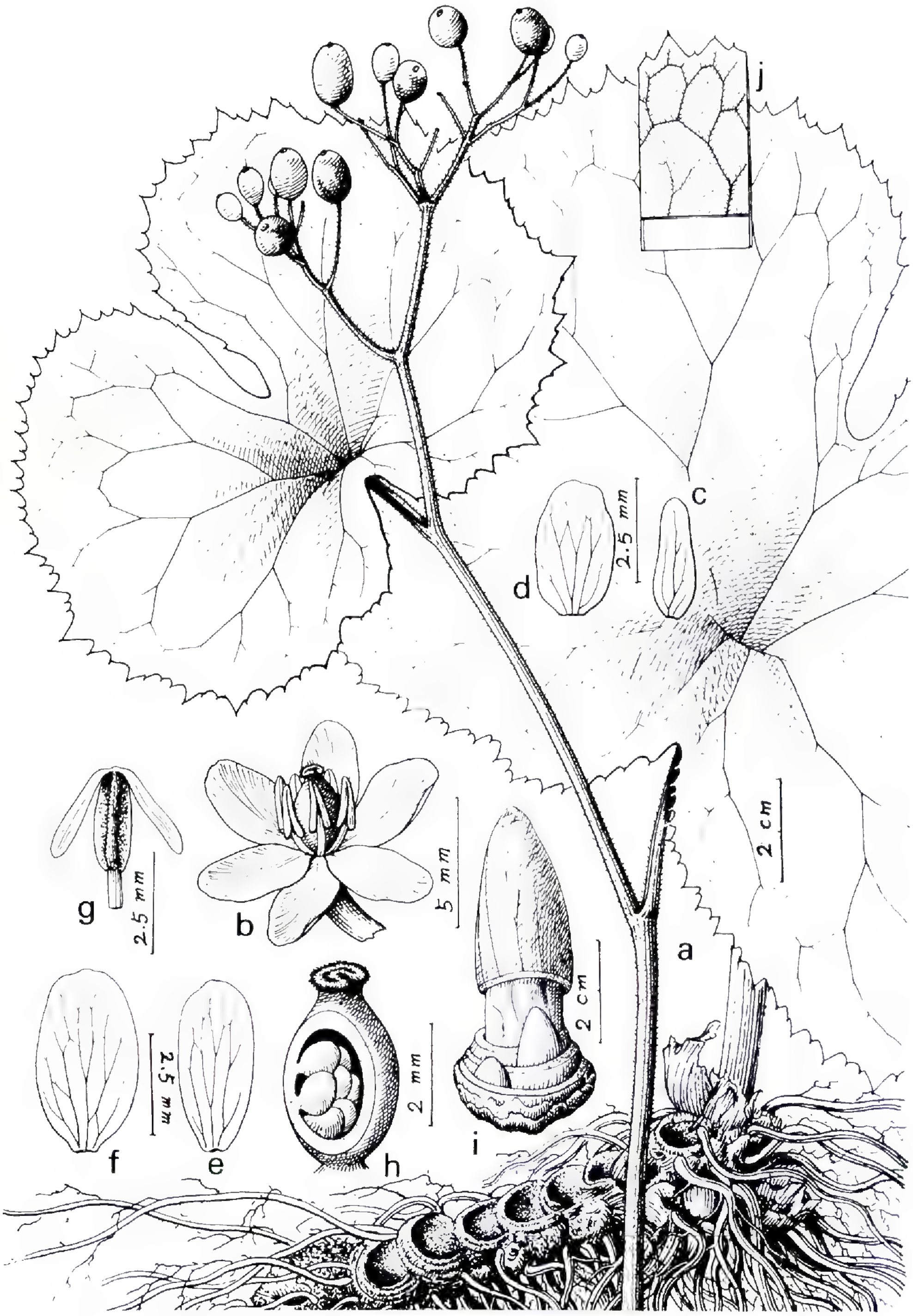


FIGURE 14. *Diphylleia sinensis* (based on *Nan-shui–Bei-diao Team 7164*, *G. X. Fu 1062*, *Shennongjia Bot. Exped. 10276*; all PE): a, upper portion of plant, rhizome, roots; b, flower; c, outer sepal; d, inner sepal; e, outer petal; f, inner petal; g, stamen; h, ovary; i, apical bud of young plant (from top of rhizome); j, undersurface of leaf.

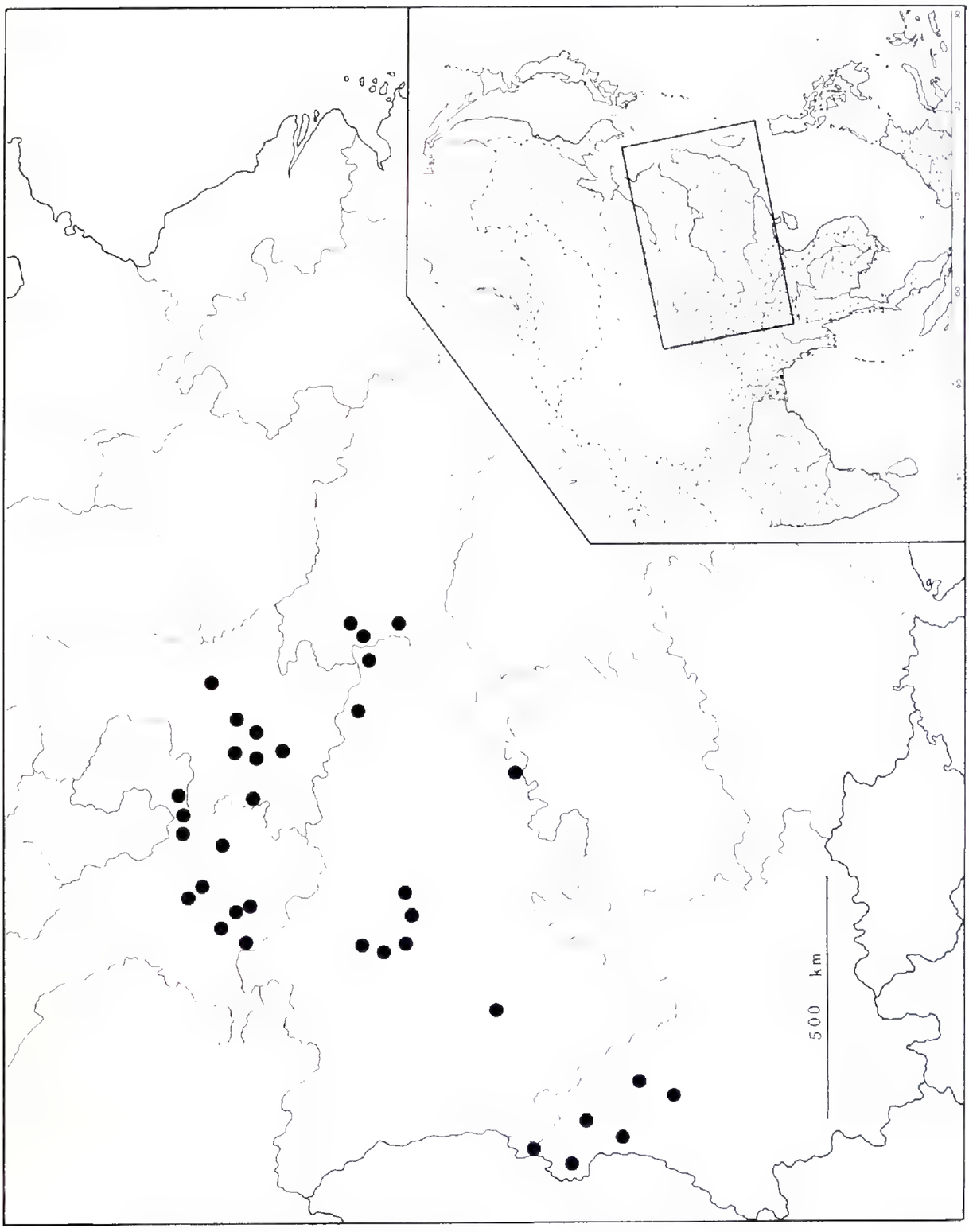
Chen 5132 (HIB), *G. X. Fu 1062* (PE), *R. H. Wang 307* (HIB); Fang, *A. Henry 6820* (BM, E, G, GH, K, NY, US), *E. H. Wilson s.n.* (W); Shennongjia Forest Distr., *Shennongjia Bot. Exped. 10276, 22868, 25107, 31388, 32451* (HIB, PE); Shennongjia Forest Distr., Xiaoshennongjia, *Shennongjia Bot. Exped. 10599* (A, HIB, PE); Shennongjia Forest Distr., vic. of Dalongtan and Xiaolongtan, *1980 Sino-Amer. Bot. Exped. 910* (A, HIB); "W Hupeh," *E. H. Wilson 2112* (W). SHAANXI: Mei Xian, *Central Shaanxi Team 85* (WUK), *Z. P. Wang 19976* (WUK); Feng Xian, *K. J. Fu 8306, 12299, 13285* (WUK); Tiabai Shan, *K. J. Fu 4452, 9424* (WUK), *P. Y. Li 5199* (WUK), *Y. M. Liang 125* (WUK), *T. N. Liou & P. C. Tsoong 330* (PE, WUK), *2263* (PE), *Qinling Team 300* (WUK), *C. L. Tang 1491* (WUK), *Z. P. Wang 15741* (WUK), *G. P. Wei 1492* (WUK); Gua-in-san, *G. Giraldi 1867* (FI); Kin-tou-san, *G. Giraldi 6004* (FI); Thae-pei-san, *G. Giraldi 6274* (FI); Hu Xian, *P. Z. Guo 386* (KUN, PE); Fuping Xian, Daping, *B. G. Guo 1421* (PE, WUK), *1769* (A, PE); Weinan, *Z. P. Wang 15632* (PE). SICHUAN: Tchen-keou Xian, *T. R. Dai 101090* (SZ), *R. P. Farges 581*[2] (K (2 sheets), P (3 sheets)). Kangding Xian, *B. C. Gao et al. 111455* (SZ); Heishui Xian, San-dao-gou, *Heishui Team 1075* (A), *1354* (PE), *X. Li 73212, 73389* (PE); Li Xian, *Z. Ho 13376* (PE), *Z. R. Wu 33348* (PE); Jinfu Shan, *Z. Y. Lau 780390* (PE), *G. F. Li 62274* (PE); Maowen Xian, *Maowen Team 2642* (PE); Heishui Xian, *Nan-shui–Bei-diao Team 01525* (PE); Mealo Xian, Ly-su-gou, *Nan-shui–Bei-diao Team 7164* (A, PE); "W Szechuan" [Wenchuan Xian, near Wasi], *E. H. Wilson 814* (GH, K, US). YUNNAN: Macul-chan, *Delavay 3862* (A, P (2 sheets)[3]), *s.n.* (K); "Yun-nan," *Delavay s.n.* (A, P), *G. Forrest 30037* (BM, E); Chungtien Plateau, *Feng 1457* (KUN); Deching Xian, *Feng 6382* (KUN, PE); Lichiang Range, NW flank, *G. Forrest 10488* (BM, E, L); Chungtien Plateau, *G. Forrest 12524* (BM, E); "duplicate of 1913–1914," *G. Forrest 15458* (E, K); "duplicate of 1917," *G. Forrest 18709* (E, US); Landsang-djiang (Mekong) & Lu-djiang (Salween), vic. of Tseku, *H. F. Handel-Mazzetti 8921* (K, W (2 sheets)); Lichiang Xian, *Lichiang Bot. Gard. 100267* (PE); Mt. Fu-Chuan, *H. D. McLaren's coll. 203* (E); Lichiang Range, *H. D. McLaren's coll. 203d* (BM); Yangtse watershed, Lichiang Snow Range, *J. F. Rock 4230* (E, US); Mt. Fu-Chuan, SW of Wei-Hsi, Mekong-Salween, *J. F. Rock 16971* (E, GH, NY, US).

The type of *Diphylleia sinensis* (*Wilson 814*, GH) is based on specimens—one in flower and one in fruit—collected at different times of the year and mounted on the same sheet. The single label bears two dates, "7/08 + 8/08." Li (1947) did not indicate a choice of elements in designating the type, but in 1951 he annotated as "isotype" a duplicate of *Wilson 814* (US) consisting only of fruiting material. Since flowering and fruiting material are about equally represented on the GH specimen and each applies equally well to the original description, we have chosen the fruiting material as the lectotype.

Although no locality more exact than "Western Szechuan" is given on the label of *Wilson 814*, it is probable that Wilson's collections of *Diphylleia sinensis* came from the area in Wenchuan Xian near Wasi ("Wa-ssu") at about 31°28′N, 103°28′E (see Clausen & Hu, 1980; Howard, 1980). This is based on the fact that Wilson's numbers *813* and *815* (*Rubus pileatus* Focke and *R. giraldianus* Focke) were both collected at that locality (Rehder, 1913; Sargent, 1916).

[2]*Farges 581* ranges from plants in bud to plants with mature fruits; the specimens were obviously collected over several months and later lumped under a single number.

[3]The specimen at A is in flower, while the 2 specimens at P are in fruit. The date on the labels is 6 August 1889, obviously an error on the A sheet.



MAP 2. Distribution of *Diphylleia sinensis* in China.

3. **Diphylleia grayi** F. Schmidt, Mem. Acad. Imp. Sci. Saint Pétersbourg **12**(2): 109. 1868. (Reis. Amurl. 109. 1868). FIGURE 15.

Diphylleia grayi F. Schmidt var. *typica* H. Takeda *in* H. Takeda & K. Tanabe, Kozan Shokobutsu Shashin-jushu, 95. *figs. 134–136.* 1931.

Diphylleia grayi F. Schmidt var. *incisa* H. Takeda *in* H. Takeda & K. Tanabe, Kozan Shokobutsu Shashin-jushu, 96. *figs. 137–139.* 1931. TYPE: no specimens were cited in the original description, and we have seen no specimens collected or annotated by Takeda as var. *incisa.* In lieu of a specimen, we designate *fig. 139* in Takeda and Tanabe (1931) as the lectotype.

Diphylleia grayi F. Schmidt var. *rotundata* H. Takeda *in* H. Takeda & K. Tanabe, Kozan Shokobutsu Shashin-jushu, 97. *fig. 140.* 1931. TYPE: no specimens were cited in the original description, and we have seen no specimens labeled as var. *rotundata* by Takeda. In the absence of a specimen, we designate *fig. 140* in Takeda and Tanabe (1931) as the lectotype.

Diphylleia cymosa Michaux subsp. *grayi* (F. Schmidt) Kitamura *in* Kitamura & Murata, Acta Phytotax. Geobot. **20:** 202. 1962.

Diphylleia cymosa Michaux subsp. *grayi* (F. Schmidt) Kitamura var. *incisa* (H. Takeda) T. Shimizu, Hikobia Suppl. **1:** 450. 1981.

Plants 2.5–9 dm tall, the stems with scattered, curled, white pubescence; growing in dense to loose colonies or sometimes individually. Lower leaf with petiole 1–25 cm long, blade 9.2–35 by 11–44 cm; upper leaf sessile or occasionally with short petiole to 1 cm long (very rarely up to 5.8 cm long), blade attached at sinus, not peltate or only slightly so, 3.9–27 by 4.8–35 cm; blades of both leaves orbicular to reniform-orbicular, margin doubly serrate and sometimes deeply lobed, pubescent beneath, sparsely so above. Peduncle 0.8–7 cm long, to 16 cm long in fruit, pubescent, sometimes densely so; inflorescence 2.2–21 cm long including peduncle, 2–8 cm broad, branches pubescent. Flowers (2 to) 4 to 16, on pedicels 0.8–3.2 cm long; outer sepals lanceolate to linear-lanceolate, 4–7.2 by 0.6–1.2 mm; inner sepals broadly elliptic, 4–9 by 3–5.4 mm; outer petals broadly obovate, 8–15 by 6–11 mm; inner petals broadly obovate, 8–15 by 4.8–11 mm; stamens ca. 4 mm long, filaments ca. 0.7–1.5 mm long, anthers ca. 2–3.2 by 0.8–1.4 mm; ovary ellipsoid, 2.5–5 by 1.7–2.8 mm, ovules 5 to 11, style 0.3–0.8 mm tall, stigma 0.2–0.7 by 0.8–1.5 mm. Berry ellipsoid to subglobose, 9–18 by 8–16 mm, blue, on pedicel 0.9–4 cm long. Seeds (3 to) 5 to 7 (to 10), ovoid to oblong, ca. 6–6.5 by 3.3–4.5 mm, rounded on all sides. Chromosome number: $n = 6$.

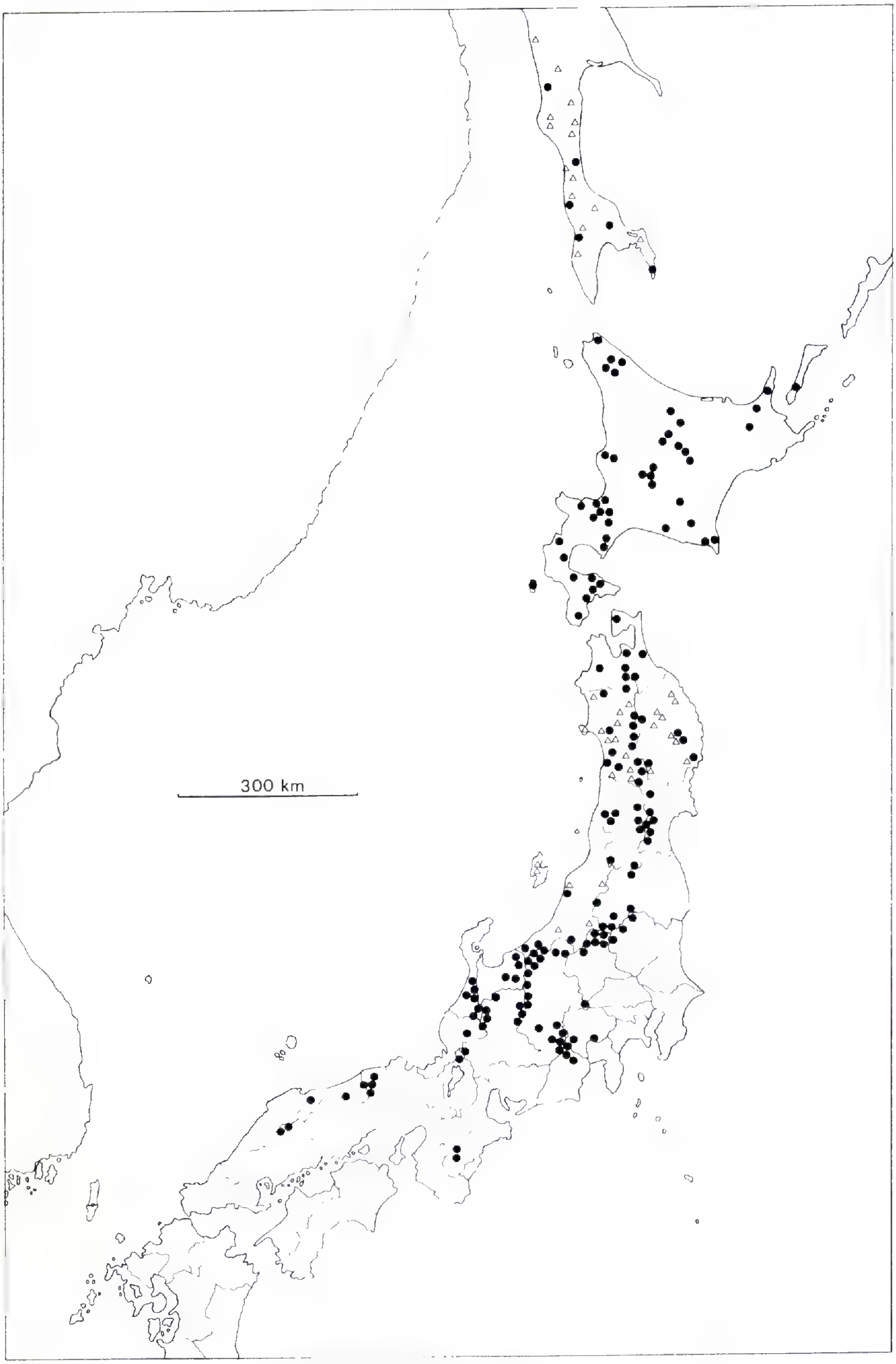
TYPE. Schmidt (1868) cited the following specimens (all from Sakhalin), which we have not seen, in his description of *Diphylleia grayi*: Arkai, 27 May 1861, *Glehn s.n.*, beginning of August 1860, *Glehn s.n.*; Dui, beginning of June 1860, and 21 July, *Glehn s.n.*; Estaing Bay, July, *Brylkin s.n.*; Kussunai, 25 April 1861 and mid-May, *Brylkin s.n.*; Manue, mid-August 1860, *without collector or number.* All are syntypes and are presumably at LE, where Glehn's and Brylkin's specimens are deposited (Holmgren, Keuken, & Schofield, 1981; Lanjouw & Stafleu, 1957; Stafleu & Cowan, 1976).

DISTRIBUTION AND ECOLOGY. Moist places in cool deciduous and coniferous forests, usually along small streams and seepages; from near sea level in the

FIGURE 15. *Diphylleia grayi* (based on *Brooks 661*, PE): a, upper portion of plant, rhizome, roots; b, flower; c, outer petal; d, inner petal; e, stamen; f, ovary.

north to 2700 m in the south. U.S.S.R. (Sakhalin, below 50°N), Japan (from Hokkaido (throughout) to southwestern Honshu (mostly limited to western side)), Kuril Islands (Kunashiri). (MAP 3.)

SPECIMENS EXAMINED. **Japan.** HOKKAIDO (Hokkaido Prefecture). "Southern Hokkaido," *W. D. Brooks 661* (PE). Abashiri Shicho: Shirataki-mura, Mt. Taira-yama, *K. Ito s.n.* (SAP); Shari-cho, Raus-daira, *S. Kobayashi s.n.*, 20 July 1967 (MAK); Shari-cho, Mt. Shari-dake, *S. Kobayashi s.n.*, 31 July 1967 (MAK); Takinoue-cho, *S. Okamoto s.n.*, 22 July 1952 (KYO); Mombetsu city, Shokotsu, *S. Okamoto s.n.*, 5 Aug. 1954 (KYO). Hidaka Shicho: Hiratori-cho, Shoya, *K. Ito s.n.*, 11 May 1963 (SAP); Shizunai-cho, Mt. Petekari-dake, *H. Koyama & N. Fukuoka 3256* (TNS); Hiratori-cho, Mt. Horoshiri-dake, *H. Koyama et al. 3591* (TNS); Samani-cho, *M. Tatewaki 9242* (SAP); Erimo-cho, Saruru-sando, *M. Tatewaki 42844* (SAP), *Y. Tokubuchi s.n.*, 14 Aug. 1892 (NY, SAP). Hiyama Shicho: Okushiri-cho, Okushiri Is., *K. Miyabe & Tokubuchi s.n.*, 28 July 1890 (K, SAP), *K. Togashi 21821* (SAP). Iburi Shicho: Muroran city, Mt. Washibetsu, *S. Kawano 444* (SAP); Shiraoi-cho, Mt. Orofure, *S. Kawano 530* (SAP). Ishikari Shicho: Sapporo city, Mt. Soranuma-dake, *S. Akiyama s.n.*, 19–20 June 1932 (NY), *H. Hara s.n.*, 18 June 1937 (TNS), *Y. Yokomizo s.n.*, 22 June 1958 (SAP); vic. of Sapporo, *S. Arimoto s.n.*, 26 May 1903 (GH, MO); Sapporo city, Jozankei, *S. Kurosawa & Y. Tateishi s.n.*, 2 June 1975 (KYO, TI, TUS), *J. Ohwi 4662* (KYO), *S. Terabayashi 588* (KYO); Eniwa city, Mt. Eniwa, *K. Miyabe s.n.*, 7 Aug. 1902 (SAP); Sapporo city, Mt. Teine-yama, *S. Saito 456* (GH), *H. Yanagishima s.n.*, 1 June 1912 (SAP); Sapporo city, *H. Takeda s.n.*, 13 May 1909 (BM, E, K, US); Mt. Moiwa-yama, *H. Takeda s.n.*, 6 June 1923 (SAP). Kamikawa Shicho: Kamikawa-cho, Mt. Taisetsu-san, *N. Kitagawa 1153* (KYO), *T. Nakai s.n.*, Aug. 1928 (TI), *J. Ohwi s.n.*, 9 Sept. 1928 (TNS), *S. Okuyama s.n.*, 18 July 1941 (TNS); Minamifurano-cho, Mt. Yubari-dake, *G. Murata & T. Yahara 37461* (KYO, SAP); Otoineppu-mura, *G. Murata et al. 38447* (KYO); Furano city, Furano, *S. Nishida s.n.*, 25 July 1916 (SAP); Kamikawa-cho, Mt. Yui-ishikari-dake, *J. Samejima & T. Misumi s.n.* (SAP). Kushiro Shicho: Teshikaga-cho, Mt. Mashu-dake, *K. Takita 297* (KYO). Nemuro Shicho: Nemuro city, Nosappu, *H. Toda s.n.*, 15 July 1954 (TUS). Oshima Shicho: Ono-cho, Naruka Valley, *F. C. Greatrex 236* (SAP); Matsumae-cho, Mt. Daisengen-dake, *T. Ishiyama 229* (SAP); Kamiiso-cho, Moheji, *S. Kaminago s.n.*, 25 May 1906 (SAP); Hakodate, *C. J. Maximowicz s.n.*, 1861 (BM, FI, G, GH, K, L, NY, US); Assabu-mura, Uzura R., *T. Nakai & Maruyama s.n.*, 22 May 1950 (TNS); Nanae-cho, Mt. Yokotsu-dake, *H. Takeda s.n.*, 21 July 1977 (KYO, TI), *I. Yamamoto 566* (SAP); Fukushima-cho, Mt. Daisengen-dake, *K. Takeda s.n.*, 24 July 1977 (NCU); Nanae-cho, Onuma, *M. Tatewaki 44602* (SAP); Yakumo-cho, Kiootoshike, *M. Tatewaki et al. s.n.*, 25 May 1955 (SAP); Oshamanbe-cho, Inaho Pass, *Y. Tokubuchi s.n.*, 16 July 1888 (SAP). Rumoi Shicho: Horonobe-cho, Toikanbetsu, *H. Koyama 1688* (KYO); Horonobe-cho, Mt. Chikoma-dake, *M. Tatewaki s.n.*, 12 July 1931 (SAP); Mashike-cho, Mt. Shokanbetsu-dake, *I. Yamamoto 5474, 5475* (SAP). Shiribeshi Shicho: Otaru, mountain gorges, *U. Faurie 201* (P), *Takenouchi s.n.*, 28 May 1928 (L); Niki-cho, Nakanosawa, *S. Ishikawa s.n.*, 2 July 1893 (SAP); Mt. Tenguyama, *Kawata s.n.*, 12 May 1935 (SAP); Shimamaki-mura, along Tomari R., *T. Misumi & J. Igarashi s.n.*, 28 June 1954 (SAP); Iwaoto, *B. Yoshimura & H. Yokoyama s.n.*, 19 June 1938 (SAP). Sorachi Shicho: Ashibetsu city, Mt. Kirigishi-yama, *E. Ishizuka & M. Tohyama s.n.*, 26 July 1970 (SAP); Ashibetsu city, Mt. Ashibetsu-dake, *H. Koidzumi 67192* (TNS); Uryu-cho, Mt. Minamishokan-dake, *G. Murata et al. 38644* (CM, KYO, SAP), *38695* (KYO, SAP); Yubari city, Mt. Yubari-dake, *J. Ohwi 5041* (KYO), *K. Sugawara s.n.*, 13 July 1969 (TUS); Yubari, *Y. Tokubuchi s.n.*, 11 Aug. 1892 (GH). Soya Shicho: Nakatonbetsu-cho, *M. Yamanoi s.n.*, 28 May 1972 (TNS); Cape Soya, *C. Wright s.n.*, 15 July 1853–1856 (GH, NY). Tokachi Shicho: Shikaoi-mura, near Lake Shikaribetsu, *M. Wakabayashi 738* (KYO). HONSHU. Mirosaki, *U. Faurie 574* (WU). Akita Prefecture: Senboku-gun, Tazawako-machi, Hachimantai, *H. Hara s.n.*, 20 July 1953 (TI), *S. Kurosawa s.n.*, 4 Aug. 1951 (TI); Senboku-gun, Tazawako-machi, Mt. Komagatake, *H. Hara s.n.*, 8 July



MAP 3. Distribution of *Diphylleia grayi* in Japan and the U. S. S. R. Dots based on specimens; triangles based on literature reports (Board of Education of Iwate Prefecture, 1970; Muramatsu, 1932; M. Noda, 1969; Sugawara, 1937).

1958 (TI), *H. Muramatsu s.n.*, 7 Aug. 1928 (TI); Yuri-gun, Chokai-machi, Mt. Chokai, *T. Kaneko s.n.*, 15 Aug. 1962 (TUS); Kitaakita-gun, Ohta-machi, Mt. Yakushi, *Kurata s.n.*, 3 June 1978 (Akita Pref. Mus.); Kazuno-gun, Kosaka-machi, Mt. Shirozi-yama, *R. Mochizuki s.n.*, 20 July 1969 (herb. Mochizuki); Hiraka-gun, Sannai-mura, Nango, *R. Mochizuki s.n.*, 3 May 1977 (herb. Mochizuki); Yuri-gun, Ouchi-machi, Shirouchi, *R. Mochizuki s.n.*, 7 May 1977 (herb. Mochizuki); Honjo city, Kitanomata, *R. Mochizuki s.n.*, 11 May 1980 (herb. Mochizuki); Senboku-gun, Nishisenboku-machi, Osawago, *R. Mochizuki s.n.*, 6 June 1981 (herb. Mochizuki); Kitaakita-gun, Tashiro-machi, Mt. Tashiro-dake, *R. Oikawa s.n.*, 25 May 1968 (TNS); Kitaakita-gun, Ohta-machi, Kitamahiru, *Takada s.n.*, 7 June 1978 (Akita Pref. Mus.); Ogachi-gun, Minase-mura, Mt. Toragayama, *Tohoku Univ. Bot. Gard. Staff s.n.*, 23 July 1970 (MO, TUS); Ogachi-gun, Ugomachi, Karuizawa, *Tsuchida s.n.*, 10 May 1974 (Akita Pref. Mus.); Ogachi-gun, Minasemura, Mt. Kiji-san, *Tsuchida s.n.*, 10 May 1974 (Akita Pref. Mus.); Akita city, Mt. Ohira-yama, *Yoshikawa s.n.*, 15 June 1955 (Akita Pref. Mus.). Aomori Prefecture: Aomori, *U. Faurie 574* (BM); Mt. Hakkoda, *U. Faurie 926* (FI), *928* (G), *13072* (MO, P); Aomori city, Hakkoda Mts., Mt. Odake, *T. Fujita & E. Nakagawa s.n.*, 1 July 1908 (TUS), *A. Kimura & S. Sugaya s.n.*, 1 July 1953 (TUS); Kamikita-gun, Towadako-machi, Hakkoda Mts., Sarukura, *K. Hasegawa s.n.*, 30 June 1964 (TI), *S. Sugaya et al. s.n.*, 2 July 1955 (TUS); Kamikita-gun, Noheji-machi, Mt. Eboshi-dake, *K. Hosi s.n.*, 17 June 1951 (KANA); Shimokita-gun, Sai-mura, *O. Mori 31* (MAK); Kamikita-gun, Towadako-machi, Mt. Towada-yama, *T. Naito 7750* (TUS); Minamitsugaru-gun, Hiraga-machi, Mt. Kushigamine, *Osawa Senior High School Students 128* (TNS); Nakatsugaru-gun, Iwaki-machi, Mt. Iwaki-san, *S. Narita s.n.*, 19 June 1910 (MAK), *H. Sakurai s.n.*, Sept. 1885 (TNS); Kamikitagun, Tohoku-mura, Kochi, *Z. Tashiro s.n.*, 1 July 1948 (KYO). Fukui Prefecture: Katsuyama city, Tani-toge Pass, *G. Koidzumi s.n.*, 7 July 1921 (KYO); Ono city, Mt. Beko-san, *Z. Tashiro s.n.*, 20 June 1937 (TNS); Nanjo-gun, Imajo-machi, Yashagaike Pond, *N. Fukuoka 4889* (KYO), *K. Ueda 508* (A, KYO, MO, TI); Katsuyama city, Mt. Tottate-yama, *S. Watanabe s.n.*, 16 May 1964 (KYO). Fukushima Prefecture: Yama-gun, Inawashiro-machi, Mt. Azuma-yama, *G. Nakahara s.n.*, June 1904 (TNS), *S. Okuyama 3558* (TNS); Minamiazumi-gun, Hinoemata-mura, Mt. Hiuchi, *G. Nakai 2587* (KYO); Minamiazumi-gun, Tateiwa-mura, Mt. Tashiro-yama, *S. Okuyama 6800* (TNS); Minamiazumi-gun, Tadami-machi, Mt. Asakusa-dake, *M. Suzuki s.n.*, 12 July 1960 (TNS); Nishishirakawa-gun, Nishisata-mura, Mt. Asahi-dake, *H. Utsumi s.n.*, 29 July 1958 (TNS); Onuma-gun, Showa-mura, Komado, *without collector or number*, 10 May 1905 (MAK). Gifu Prefecture: Ibi-gun, Sakauchi-mura, SW of Mt. Sobatsubu-yama, *N. Fukuoka 5793* (KANA, KYO); Ono-gun, Shirakawa-mura, Hirase, *M. Hashimoto 382* (KANA); Ono-gun, Shokawa-mura, Tenbu Pass, *J. Hatasa s.n.*, 25 July 1968 (TNS); Ibi-gun, Kasuga-mura, E of Mt. Ibuki-yama, *M. Hutch 23487* (KYO), *Y. Satake & S. Okuyama s.n.*, 24 May 1942 (TNS); Ono-gun, Takane-mura, Nomugi Pass, *H. Kanai s.n.*, 13 June 1958 (MAK), *H. Kanai & H. Ohashi 731217* (TNS); Ibi-gun, Sakauchi-mura, Kawakami, *H. Kanai & T. Morita 0259* (TI); Masuda-gun, Kasako-cho, NW of Mt. Ontake-san, *G. Murata 10670* (KYO); Yoshiki-gun, Mannami, *Y. Nagai s.n.*, 31 May 1972 (KANA, MAK), *N. Naruhashi 3616* (KANA); Gujo-gun, Takawashi-mura, Mt. Daihi-dake, *S. Ueno s.n.*, 22 July 1970 (TNS). Gunma Prefecture: Shimizu-toge Pass, *U. Faurie 2396* (MO); Tone-gun, Kaashina-mura, Oze, *T. Harazawa s.n.*, 1 Aug. 1910 (MAK), *M. Mizushima 1121* (TI), *G. Nakai 2628* (KYO), *S. Okuyama s.n.*, 21 July 1934 (TNS), *M. Ono s.n.*, 2 June 1954 (TI); Tone-gun, Minakami-machi, Mt. Tanigawa, *M. Furuse s.n.*, 16 June 1958, 6 June 1961 (A), *K. Hasegawa s.n.*, 15 July 1966 (TI), *K. Hisauchi 489* (TI), *H. Kanai 3368* (TI), *T. Miyamae s.n.*, 30 May 1969 (TNS), *R. Noguchi s.n.*, 24 June 1934 (TNS), *S. Okuyama 13055* (TNS), *T. Yamazaki s.n.*, 24 June 1944 (TI); Tone-gun, Minakami-machi, Mt. Hotaka, *H. Kanai s.n.*, 5 July 1957 (TI); Tone-gun, Minakami-machi, Mt. Hiraga-take, *H. Kanai s.n.*, 1 Aug. 1959 (TI); Azuma-gun, Himekoi-mura, Hiramata, *K. Matsuda 378* (TNS); Tone-gun, Kaashina-mura, Mt. Shirane, *H. Ohba & S. Akiyama 1317* (A, KYO, TI); Tone-gun, Niiharu-mura, Mikuni Pass, *S. Okuyama et al. s.n.*, 11

July 1957 (TNS). Hiroshima Prefecture: Hiba-gun, Mt. Sarumasa-yama, *G. Akiyama s.n.*, 23 May 1976 (TNS); Mt. Omaki-san, *S. Takafuji 583* (KYO). Hyogo Prefecture: Kinosaki-gun, Hidaka-cho, Mt. Sofugatake, *E. Araki 3123* (KYO); Mikata-gun, Muraoka-cho, Mt. Torokawa-yama, *E. Araki s.n.*, 12 July 1931, 31 August 1931 (KYO), *M. Hashimoto 9223* (KYO), *G. Koidzumi s.n.*, July 1927 (KYO), *G. Murata 20902* (KYO); Mikata-gun, Onsen-cho, Mt. Ogino-sen, *S. Hosomi s.n.*, 31 July 1968, 4 May 1969 (KYO); Yabu-gun, Sekinomiya-cho, Mt. Hyono-sen, *G. Murata & K. Iwatsuki 700* (KYO, TNS), *J. Ohwi s.n.*, 6 July 1927 (TNS), *S. Terabayashi 60* (KYO), *Y. Yoneda s.n.*, 13 May 1933 (KYO). Ishikawa Prefecture: Kanazawa city, Komagaeri-Kurotani, Mt. Takasaburo-yama, *N. Fukuoka 7658* (KYO); Kanazawa city, Mt. Takao, *H. Kaneko s.n.*, 20 May 1962 (KANA, MAK); Ishikawa-gun, Shiramine-mura, Mt. Haku-san, *U. Faurie? 2798* (P), *M. Hotta 5707, 5936, 5950* (KYO), *G. Koidzumi s.n.*, 8 July 1921 (KYO), *J. Ohwi s.n.*, 25 April 1929 (TNS), *S. Terabayashi 73, 74* (KYO), *K. Urabe s.n.*, Aug. 1908 (KYO); Ishikawa-gun, *H. Nakagawa 372* (KANA); Kanazawa city, Mt. Ioh-sen, *N. Satomi s.n.*, 27 May 1951 (TI); Ishikawa-gun, Oguchi-mura, Iwama Hot Spring, *N. Satomi s.n.*, 16 June 1952 (KANA). Iwate Prefecture: Shimohei-gun, Kawai-mura, Mt. Hayachine, *R. Endo s.n.*, 31 July 1951 (TUS), *E. Ito & M. Togashi 38* (TNS), *G. Murata & H. Tabata 222* (KYO), *J. Murata et al. 5827* (TI), *Y. Ogura s.n.*, 19 June 1910 (MAK), *S. Okuyama 12807* (TNS), *K. Sohma 3241* (MO); Iwate-gun, Mt. Iwate, *M. Honda s.n.*, 27 July 1927 (TI), *G. Nakahara s.n.*, 26 July 1907 (TI), *Y. Ogura s.n.*, 4 Aug. 1915 (TI), *H. Sakurai s.n.*, 29 July 1908 (A); Waka-gun, Iwasaki-mura, Mt. Ushigata-yama, *K. Hosoi s.n.*, 20 July 1948 (KANA); Iwate-gun, Shizukuishi-machi, Mt. Komagatake, *H. Iwabuchi 2379* (TUS); Kamaishi city, Mt. Goyo-san, *H. Koyama & M. Hotta 2270* (TNS), *H. Koyama & S. Sasamura 2539* (KYO, TNS); Nambu, *Tschonoski s.n.*, 1865 (GH, K). Miyagi Prefecture: Katta-gun, Zao-machi, Mt. Zao, *K. Endo s.n.*, 12 June 1900 (MAK), *H. Kanai 742732* (A, BM, E, KYO, L, NY, TNS, WU), *M. Kato 54* (MAK); Natori-gun, Akiu-machi, Mt. Daito-dake, *H. Ohashi s.n.*, 3 May 1959 (TUS); Natori-gun, Akiu-machi, Mt. Takakura-yama, *H. Ohashi 3348* (TI, TUS); Izumi city, Mt. Izumigatake, *K. Saito & T. Keneko s.n.*, 18 May 1961 (TUS); Tamatsukuri-gun, Naruko-machi, Kawatabi, *K. Sugawara 8517* (TUS); Shibata-gun, Kawasaki-machi, Sasaya, *S. Sugaya et al. s.n.*, 26 May 1971 (TUS); Kurokawa-gun, Yamato-machi, Mt. Funagata, *M. Yashima & H. Ohba 717011* (TUS). Nagano Prefecture: Minamisaku-gun, Kawakami-mura, Jumonji Pass, *H. Asuyama s.n.*, 11 July 1930 (TNS); from Mitsumata to Mt. Jonen-dake to Mt. Choga-dake, *D. E. Boufford et al. 19951* (MO); Kamiminochi-gun, Togakushi-mura, Mt. Togakushi, *S. Ito 132* (TNS), *H. Koidzumi 67178* (TNS), *S. Matsuda s.n.*, 28 July 1893 (KYO), *H. Takeda s.n.*, 19 July 1904 (E, K), *C. Wright s.n.*, 1853–1856, (K); Kamiminochi-gun, Kinasa-mura, Okususobana, *S. Ito 152* (TNS); Minamiazumi-gun, Azumi-mura, Mt. Norikura-dake, *T. Ito s.n.*, 19 Aug. 1891 (TI); Kamiina-gun, Hase-mura, Mt. Senjo-dake, *K. Iwatsuki et al. 120* (KYO), *G. Murata 8275* (KYO), *T. Yamazaki s.n.*, 3 Aug. 1949 (TI); Kiso-gun, Oshika-mura, Mt. Akaishi-dake–Mt. Osawa-dake, *K. Iwatsuki & H. Koyama 183* (KYO); Shimoina-gun, Achi-mura, Mt. Ena-san, *H. Kanai s.n.*, 29 July 1957 (TI); Shimotakai-gun, Yamanouchi-cho, Shigakogen, *H. Kanai 7607* (TI); Shimoina-gun, Oshika-mura, Ogawara, *T. Kawamata 65* (TNS); Minamiazumi-gun, Azumi-mura, Tokugo Pass, *G. Koidzumi s.n.*, 31 May 1928 (KYO), *T. Nakai s.n.*, 11 July 1927 (TI); Minamiazumi-gun, Azumi-mura, Kamikochi, *K. Kojima s.n.*, 6 July 1934 (KYO), *K. Ueda et al. 19* (KYO); Kiso-gun, Oshika-mura, Sanpuku Pass, *F. Konta 10326* (KYO), *J. Sugimoto 4915* (TI); Nishikomaga-dake, *M. Kume 2595* (A); Kitaazumi-gun, Hakuba-mura, Mt. Shirouma, *T. Makino s.n.*, Aug. 1918 (MAK), *N. Maruyama s.n.*, 2 Aug. 1950 (TNS), *M. Sugiyama s.n.*, 29 June 1968 (TI), *S. Terabayashi 306, 793* (KYO), *F. Tomihisa s.n.*, 16 Aug. 1923 (KYO), *Y. Yabe s.n.*, 26 Aug. 1902 (TI); Kitaazumi-gun, Hakujo-mura, to Sarukura from Futamata, foot of Mt. Shirouma, *M. Furuse s.n.*, 25 May 1958 (A); Kiso-gun, Minamishinano-mura, Mt. Hijiri-dake, *H. Matsuda s.n.*, 17 June 1954 (TI); Omachi city, Taira-mura, *T. Mimoro et al. 1492* (TNS); Shimotakai-gun, Kijimadaira-mura, Kayanodaira, *M. Mizushima s.n.*, 16 June 1966 (A, KYO, MAK, TI); Kiso-gun, Oshika-mura, Mt. Otaka-san, *M. Muramatsu 1487* (TNS); Ki-

taazumi-gun, Otari-mura, Mt. Amakazari, *D. E. Boufford & E. W. Wood 19145* (A), *G. Murata et al. 30378* (KYO), *S. Terabayashi 767* (KYO), *S. Tsugaru 3389* (MO); Minamiazumi-gun, Hotaka-mura, Mt. Tsubakuro, *Y. Ogura s.n.*, 25 June 1918 (TI), *Y. Satake s.n.*, 13 July 1941 (TNS); Kamiina-gun, Hase-mura, Mt. Kitaarakawa-dake, *Y. Okada s.n.*, 12 Aug. 1923 (TNS); Chino city, Mt. Yatsuga-take, *C. Okawa s.n.*, 4 July 1977 (TNS), *Y. Yabe s.n.*, 20 Aug. 1902 (TI); Minamiazumi-gun, Azumi-mura, Mt. Otaki, *S. Okuyama et al. s.n.*, 18 Aug. 1954 (TNS); Kamiina-gun, Hase-mura, Mt. Komaga-take, *H. Sakurai s.n.*, 10 Sept. 1884 (TNS); Kiso-gun, Oshika-mura, Mt. Toyoguchi-san, *T. Yamazaki s.n.*, 29 July 1953 (TI); Kiso-gun, Agematsu-mura, Mt. Kisokoma-dake, *without collector or number*, July 1935 (MAK). Nara Prefecture: Mt. Sanjogatake–Mt. Inamuragatake–Gyojagaeri, *H. Hara s.n.*, 15 July 1955 (TI), *M. Hotta et al. 55* (KYO), *G. Murata & K. Iwatsuki 72* (KYO), *Y. Momiyama s.n.*, 16 July 1955 (TI); Yoshino-gun, Tenkawa-mura, Omine Mts., Mt. Misen-Gyojagaeri, *M. Hotta et al. 74* (KYO), *M. Hotta & N. Fukuoka 258* (KYO), *G. Koidzumi s.n.*, 14 July 1922 (KYO), *G. Murata & T. Shimizu 88* (KYO), *H. Okada et al. 1370* (KYO), *S. Tanaka s.n.*, 17 July 1933 (K, TNS), *Yokohama Nursery Co. s.n.*, Aug. 1907 (E). Niigata Prefecture: Nishikanbara-gun, Yahiko-mura, Mt. Yahiko, *N. Fukuoka 1828* (KYO); Nishikubiki-gun, Myokokogen-cho, Mt. Kurohime-yama, *N. Fukuoka 2158* (KYO); Nishikubiki-gun, Myokokogen-cho, Mt. Myoko-san, *S. Matsuda s.n.*, 27 July 1894 (KYO), *G. Murata 6834* (KYO); Nishikubiki-gun, Myokokogen-cho, Sasagamine, *A. Nitta 10681* (KYO); Nakauonuma-gun, Tsunami-mura, Mt. Naeba, *S. Okuyama s.n.*, 19 July 1936 (TNS), *Y. Satake & H. Ito s.n.*, 12 July 1951 (TNS). Shiga Prefecture: Higashiasai-gun, Asai-cho, Takayama-Torigoe Pass, *Y. Inamasu & N. Fukuoka 82* (KYO); Ika-gun, Suino-mura, Mt. Tsuchigura, *Y. Inamasu & N. Fukuoka 205* (KANA, KYO); Higashiasai-gun, Ibuki-cho, Mt. Ibuki, *G. Koidzumi s.n.*, 26–27 June 1922 (KYO); Higashiasai-gun, Asai-cho, Mt. Kanakuso, *G. Murata & N. Fukuoka 1020* (E, K, KANA, KYO, MAK, MO, TNS); Takashima-gun, Imazu-cho, Mt. Miedake, *S. Watanabe s.n.*, 26 June 1927 (KYO). Shimane Prefecture: Iishi-gun, Yoshida-mura, Mt. Omaki-san, *Y. Moriyama s.n.*, 5 Aug. 1961 (MAK). Shizuoka Prefecture: Shizuoka city, Mt. Hakkorei, *F. Konta et al. 309* (KYO); Shizuoka city, Mt. Senmai, *H. Matsuda s.n.*, 7 July 1954 (TI); Shizuoka city, Higashimata, *H. Matsuda s.n.*, 22 July 1954 (TI). Tochigi Prefecture: Nikko city, Mt. Shirane-yama, *J. Bisset 4027* (E), *Hattori s.n.*, 1 July 1922 (TI), *T. Makino s.n.*, 17 July 1924 (MAK), *H. Sakurai s.n.*, 16 July 1887 (TNS); Shioya-gun, Fujiwaramachi, Mt. Takahara-yama, *H. Kanai s.n.*, 25 May 1959 (TI); Nikko city, Yumoto, *S. Kobayashi 45870* (MAK), *G. Murata 18205* (KYO), *N. Shibusa s.n.*, 2 July 1966 (TNS), *S. Suzuki s.n.*, 21 June 1931 (KYO); Nikko, *Yokohama Nursery Co. s.n.*, Aug. 1906 (E). Tottori Prefecture: Saihaku-gun, Daisen-cho, Mt. Daisen, *S. Hori s.n.*, 4 Aug. 1889 (MAK), *N. Kinashi s.n.*, 7 June 1917 (KYO), *G. Koidzumi s.n.*, 3 July 1924 (KYO); Yazu-gun, Sajimura, Kitadani, *G. Murata et al. 298* (KYO). Toyama Prefecture: Shimoshinkawa-gun, Asahi-cho, Mt. Iburi, *H. Kanai s.n.*, 1 Aug. 1958 (TI); Higashitonami-gun, Minoya-mura, *H. Kaneko s.n.*, 19 May 1963 (KANA, TI); Nakashinkawa-gun, Kaminoichi-cho, Mt. Takamine-yama, *N. Kurosaki 1601* (KANA, KYO); Nakashinkawa-gun, Tateyama-cho, Mt. Tateyama, *S. Matsuda s.n.*, Aug. 1893 (KYO), *G. Nakai 4000* (KYO); Higashitonami-gun, Kamitaira-mura, Bunao Pass, *T. Mimoro & S. Tsugaru 11846* (MO, TNS), *G. Murata 30018* (KYO, TNS); Higashitonami-gun, Kamitaira-mura, Hosoo Pass, *N. Mino s.n.*, 21 May 1964 (KANA); Shimoshinkawa-gun, Unazuki-cho, Mt. Karamatsu, Baba-dani valley, *G. Murata & T. Shimizu 1904* (KYO), *J. Ohwi 7107* (KYO), *S. Okamoto s.n.*, 23 July 1935 (KYO); Higashitonami-gun, Nawaga-ike Pond, *N. Satomi 10150* (KANA, MAK, TNS). Yamagata Prefecture: E of Higashine city, Makino to Mt. Shiragami, *D. E. Boufford et al. 22281* (GA, GH); Yamagata city, Yamadera, *K. Doi s.n.*, 10 Aug. 1966 (TNS), *H. Ohashi s.n.*, 20 May 1960 (TUS); Higashitagawa-gun, Tachikawa-machi, Mt. Gassan, *R. Endo s.n.*, 28 July 1914 (TUS); Nishimurayama-gun, Nishikawa-machi, Mt. Asahi-dake, *Hara s.n.*, 7 July 1959 (TI); Nishiokitama-gun, Oguni-machi, Mt. Iide, *M. Ito 407* (KYO, MO), *G. Koidzumi s.n.*, 15 Aug. 1910 (TI), *H. Ohba et al. 73071* (A, TI, TUS), *T. Yamazaki s.n.*, 3 Aug. 1943 (TI), *T. Yamazaki et al. 15* (TI); Higashitagawa-gun, Asahi-mura, Kamina, *K. Mori s.n.*, 30 July 1950 (TI); Nishiokitama-gun, Oguni-machi, Oishisawa,

S. Terabayashi 828 (KYO); Akumi-gun, Yuza-machi, Mt. Chokai, *Univ. Tokyo Staff s.n.*, 28 July 1888 (TI); Nishimurayama-gun, Nishikawa-machi, Mt. Yudono, *Univ. Tokyo Staff s.n.*, 23 July 1882 (G, TI); Yonezawa city, Mt. Azuma-san, *Yoshida s.n.*, 6 Aug. 1915 (MAK). Yamanashi Prefecture: Kitakuma-gun, Shirasu-cho, Mt. Kanno-dake, *S. Kitamura s.n.*, 28 July 1931 (KYO), *H. Matsuda s.n.*, 22 July 1954 (TI), *Y. Ogura s.n.*, 28 July 1920 (TI); Kitakuma-gun, Shirasu-cho, Mt. Komaga-take, *G. Murata 11976* (KYO); Nakakuma-gun, Ashiyasu-mura, Mt. Kita-dake, *H. Terao 895* (KYO); "Fudzi yama" [Mt. Fuji-san], *Tschonoski s.n.*, 1864 (BM, P, UPS, W). **Kuril Islands.** KUNASHIRI: *without collector or number*, 1935? (KYO). **U.S.S.R.** SAKHALIN. Without further locality: *Augustinowicz 18591* (BM), *Augustinowicz s.n.* (G, GH, K). Maoka Province: Maoka-gun, Mt. Maoka-san, *T. Miyake s.n.*, 4 June 1907 (SAP); Katada-gun, Mt. Nota-san, *T. Miyake s.n.*, 28 June 1907 (SAP). Motodamari Province: Motodamari-gun, Mt. Tasso-san, *M. Nagai & S. Iwadera s.n.*, 23 July 1927 (SAP). Odomari Province: Nagahama-gun, Shiretoko-mura, Mt. Shiretoko, *T. Miyake s.n.*, 11 July 1908 (SAP, TNS). Shikika Province: Sanko-gun, Funadomari, *M. Tatewaki 22705, 22961* (KYO, SAP). Tomari Province: Nayoshi-gun, Nayoshi-mura, Kitakosawa, *M. Henmi 63* (MAK). Toyohara Province: Toyohara-gun, Mt. Suzuya-dake, *T. Miyake s.n.*, 27 July 1907 (SAP), *M. Sato s.n.*, 19 July 1932 (TI).

We have seen no collections of *Diphylleia* from the Amur region of the Soviet Far East. The reports of its occurrence there by Kumazawa (1930), Li (1947), and others appear to be based on the title of the publication in which *D. grayi* was first described (*Reisen in Amur-lande und auf der Insel Sachalin*), rather than on actual specimens. Fedchenko (1937), in his treatment of the Berberidaceae for *Flora SSSR*, attributed *Diphylleia* to only Sakhalin in the Soviet Union.

Takeda (*in* Takeda & Tanabe, 1931) named plants with very deeply lobed leaves *Diphylleia grayi* var. *incisa*, and those with the lobes essentially lacking var. *rotundata*. The degree of lobing of the leaves in *D. grayi* is variable and continuous; plants with both deeply lobed and nearly unlobed leaves can be found intermixed in single populations. *Kanai 742732* represents plants with lobed and unlobed leaves. There seems to be no basis for the recognition of these plants as infraspecific taxa.

Takeda (*in* Takeda & Tanabe, 1931) did not cite specimens or indicate types in his descriptions of *Diphylleia grayi* vars. *incisa* and *rotundata*, and we have seen no specimens annotated or collected by him with these varietal names. In lieu of specimens, we wish to designate the illustrations accompanying the original descriptions of these two varieties as the lectotypes.

In the more than 200 specimens of *Diphylleia grayi* that we examined, seven had upper petioles longer than 1 cm (1.2 cm, 1.3 cm, 1.4 cm, 1.6 cm, 2.1 cm, 4.4 cm, and 5.8 cm). The most logical explanation for these aberrant plants is that although they have only two leaves, they represent forms transitional between plants with two and plants with three leaves. In the occasional plants with three leaves, the uppermost leaf is sessile or subsessile while the next lower leaf is petiolate.

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APPENDIX 1. **Voucher specimens of Diphylleia used in anatomical studies.**

TAXON	VOUCHER
D. cymosa	U. S. A., North Carolina, Avery County, *E. W. Wood & Boufford 4150a* (BM, CM, KYO) U. S. A., North Carolina, Watauga County, *Boufford & E. W. Wood 20954* (CM, KYO)
D. grayi	Japan, Honshu, Hyogo Prefecture, Mt. Hyonosen, *S. Terabayashi 60* (KYO) Japan, Honshu, Ishikawa Prefecture, Mt. Haku-san, *S. Terabayashi 73, 74* (KYO) Japan, Honshu, Nagano Prefecture, Mt. Shirouma, *S. Terabayashi 793* (KYO) Japan, Honshu, Yamagata Prefecture, Mt. Iide, *M. Ito 40* (KYO)
D. sinensis	China, Hubei Province, Shennongjia Forest District, *Wan Jiziang* (material in fruit; no voucher collected)

APPENDIX 2. **Voucher specimens of Diphylleia used for pollen observations.**

TAXON	VOUCHER
D. cymosa	U. S. A., North Carolina, Watauga County, Potato Hill, N of jct. of state roads 1324 and 1306, *Kologiski & Perino 165* (GH) U. S. A., Virginia, Smyth County, NE slope of White Top Mt., *J. K. Small s.n.*, 28–29 May 1892 (GH) U. S. A., North Carolina, Macon County, 13 mi N of U.S. 64 on Rainbow Springs–Aquone Forestry Rd., *Radford 5239* (NCU)
D. grayi	Japan, Honshu, Iwate Prefecture, Mt. Hakkoda, *A. Kimura & S. Sugaya s.n.*, 3 July 1952 (TUS) Japan, Honshu, Miyagi Prefecture, Mt. Izumi, *K. Saito & T. Kaneko s.n.*, 18 May 1961 (TUS) Japan, Honshu, Nagano Prefecture, Minamiazumi-gun, *H. Takahashi 366* (TUS)
D. sinensis	China, Gansu Province, "SE Gansu," *Licent 5325* (BM) China, Sichuan Province, Mealo Xian, Lysugou, *Nan-shui–Beidiao Team 7164* (PE) China, Yunnan Province, "Ma-cul-chan," *Delavay 3862* (A)

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ADDENDUM. **Lectotypification of Diphylleia grayi F. Schmidt.**

Since this paper went to press, one of us (D. E. B.) has had the opportunity to examine the following specimens from Sakhalin, U. S. S. R., that were cited by Schmidt (1868) in his original description of *Diphylleia grayi*: no further locality, *Glehn s.n.*, beginning of August 1860; Dui, *F. Schmidt s.n.*, June 1860 (Schmidt did not indicate in the protologue that his collections were among those used in the original description, but the specimen cited as "Dui Anf. Juni 1860" is probably this one), *Glehn s.n.*, 21 July 1860; Arkai, *Glehn s.n.*, 27 May 1861; Kussunai, *Brylkin s.n.*, May 1860, *Brylkin s.n.*, 25 April 1861 (all at LE).

There are two plants on the sheet collected by *Glehn* on 21 July 1860, and both are atypical of the vast majority of *Diphylleia grayi* in having a petiolate upper leaf. It is almost certain, however, that Schmidt based his description of the fruits of *D. grayi* on this specimen, since none of the other specimens contains mature fruits. Of the other specimens, *Brylkin s.n.*, 25 April 1861, is a sterile plant, and the *Schmidt* specimen has no flowers and only very young fruits. *Glehn s.n.*, beginning of August 1860, is a mixed collection containing an upper leaf and infructescence (berries lacking) from one plant and the upper portion of another plant with two leaves and flowers, which must have been collected in the spring and not on the date indicated on the label. The specimen collected at Kussunai, *Brylkin s.n.*, May 1860, has only a single late flower and several very immature fruits and could not have been the source for Schmidt's description of floral characters. The remaining sheet, *Glehn s.n.*, 27 May 1860, collected at Arkai, contains two very young plants with flowers in various stages of development; these were clearly the basis for Schmidt's comments on the sepals, and for his comparison of them with those of *D. cymosa* Michaux, in his original description. There is also a small packet on this sheet that contains what appear to be portions of the roots of one of the plants.

Of the two specimens on this sheet, the one on the right is the more complete, and it is this one that I wish to designate as the lectotype of *Diphylleia grayi* F. Schmidt. Photographs of the lectotype have been deposited at A, KYO, and PE.

I am grateful to the director and curators at LE for making these specimens available to me on loan.—D. E. B.

A POSSIBLE MAGNOLIOID FLORAL AXIS, LOISHOGLIA BETTENCOURTII, FROM THE UPPER CRETACEOUS OF CENTRAL CALIFORNIA

VIRGINIA M. PAGE

THE FOSSIL SPECIMEN described below was collected from an outcrop of Upper Cretaceous marine sediments in the foothills of the Diablo Range on the western border of the San Joaquin Valley near the central California town of Patterson. This locality, locally known as Black Gulch, has yielded numerous specimens of petrified woods (described in Page, 1967, 1968, 1970, 1973, 1979, 1980, 1981), as well as phosphatic concretions containing well-preserved pollen, spores, dinoflagellates, foraminifera, and radiolarians. According to Bishop (1970), the sampled sequence at Black Gulch is correlated with zone D-2 of the foraminiferal zones established by Goudkoff (1945) and is equivalent to the Ragged Valley Shale member of the Moreno Formation. Due to a discrepancy in opinion regarding the position of the Maastrichtian-Campanian boundary with respect to the foraminiferal zones of Goudkoff, there is a lack of agreement as to the age of the D-2 zone, and hence of the Black Gulch locality. Whereas most workers place the boundary between Goudkoff's D-2 and E zones, Bishop (*in* Chmura, 1973) stated that he believes the boundary to occur very near the D-1 and D-2 division. Since the Black Gulch locality lies within the D-2 zone, it is Maastrichtian in age according to most workers, but Campanian according to Bishop. Chmura (1973), who analyzed angiosperm pollen obtained from concretions, accepted Bishop's judgment, but Stein (1983) found that the concretions contain a typical Maastrichtian assemblage of dinoflagellates. The opinion of the majority of workers is adopted here.

The specimen is a calcareous petrifaction that measured approximately 3.5 cm in diameter and 3 cm in length before it was sectioned. Most of the tissues had been extensively altered, partly by pressure but chiefly by microorganisms, prior to fossilization. The general morphology is that of a herbaceous stem: a pith surrounded by a ring of vascular bundles and a cortex (FIGURE 1). The epidermis was not preserved. The pith is about 1.5 cm in diameter. Although much of the center has been destroyed, the cells—except for a peripheral zone of mostly small, relatively thick-walled ones—appear to have been large and thin walled. Numerous large cells averaging 102 μm in diameter occur individually in the peripheral zone; each is surrounded by small, flattened cells. Lenticular plates of sclereids are abundantly scattered throughout. As seen in longitudinal section, these plates are about 1 cm long and 0.5 cm thick. It is difficult to determine the shape of individual sclereids, for they are closely packed and variously convoluted (FIGURE 2). Some, at least, are branched,

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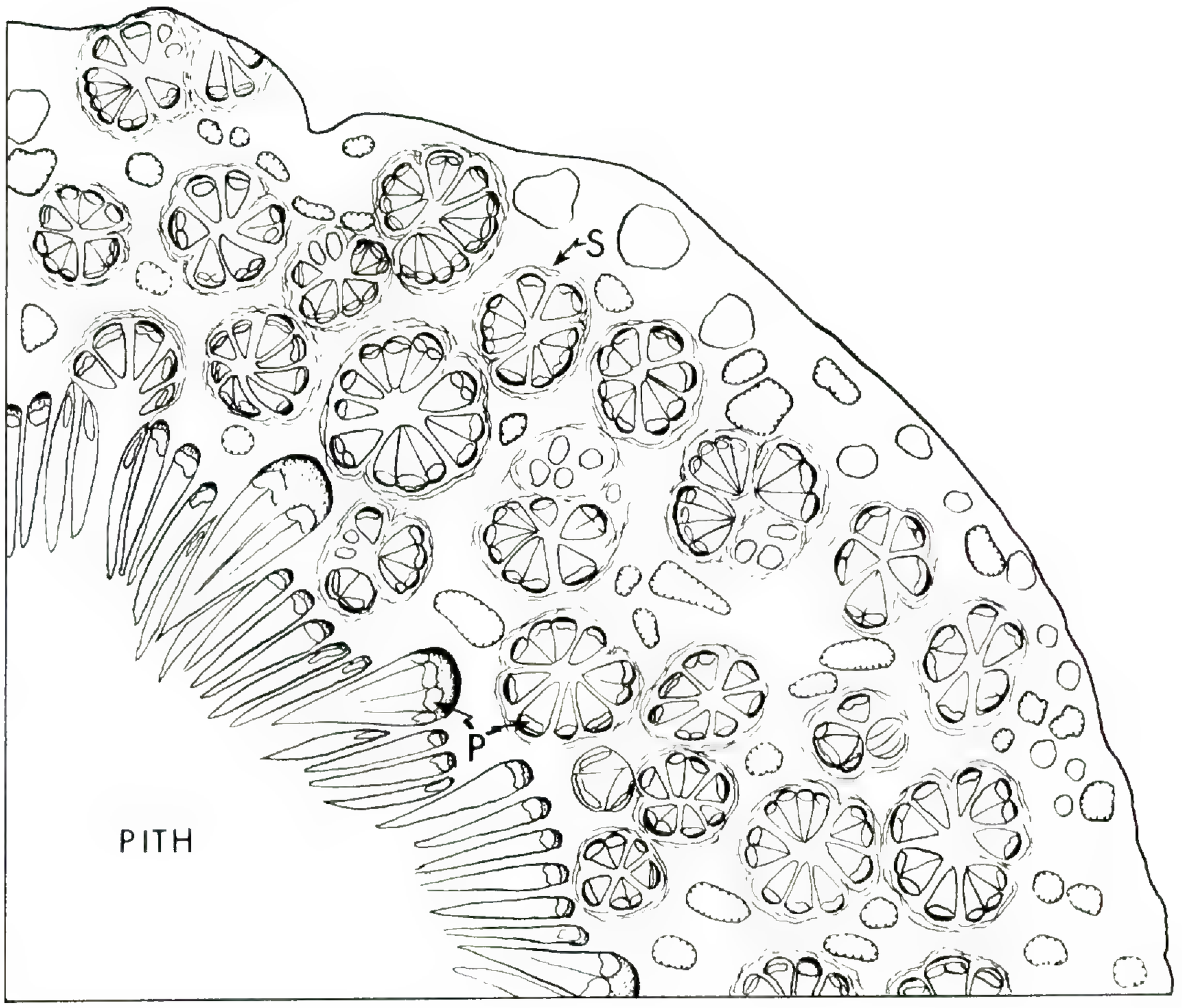


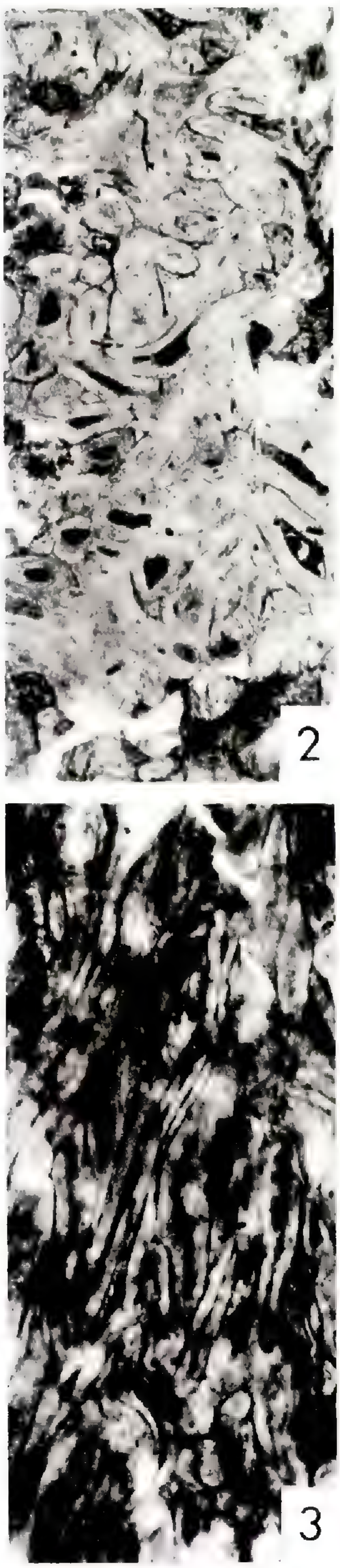
FIGURE 1. **Loishoglia bettencourtii:** diagram of quadrant in transverse section showing arrangement of vascular bundles, × 6. Those aligned at periphery of pith are stelar. Note enlarged fascicles in various stages of division and departure from stele. Stippled portions of large fascicles denote phloem fibers and crushed phloem cells. Circles of bundles in cortex show variety of patterns. Disrupted bundle circles and atrophied bundles appear as outlines, nests of sclereids as outlines with stippled borders. Pith sclereids not shown. P = phloem cavities, S = "sheath."

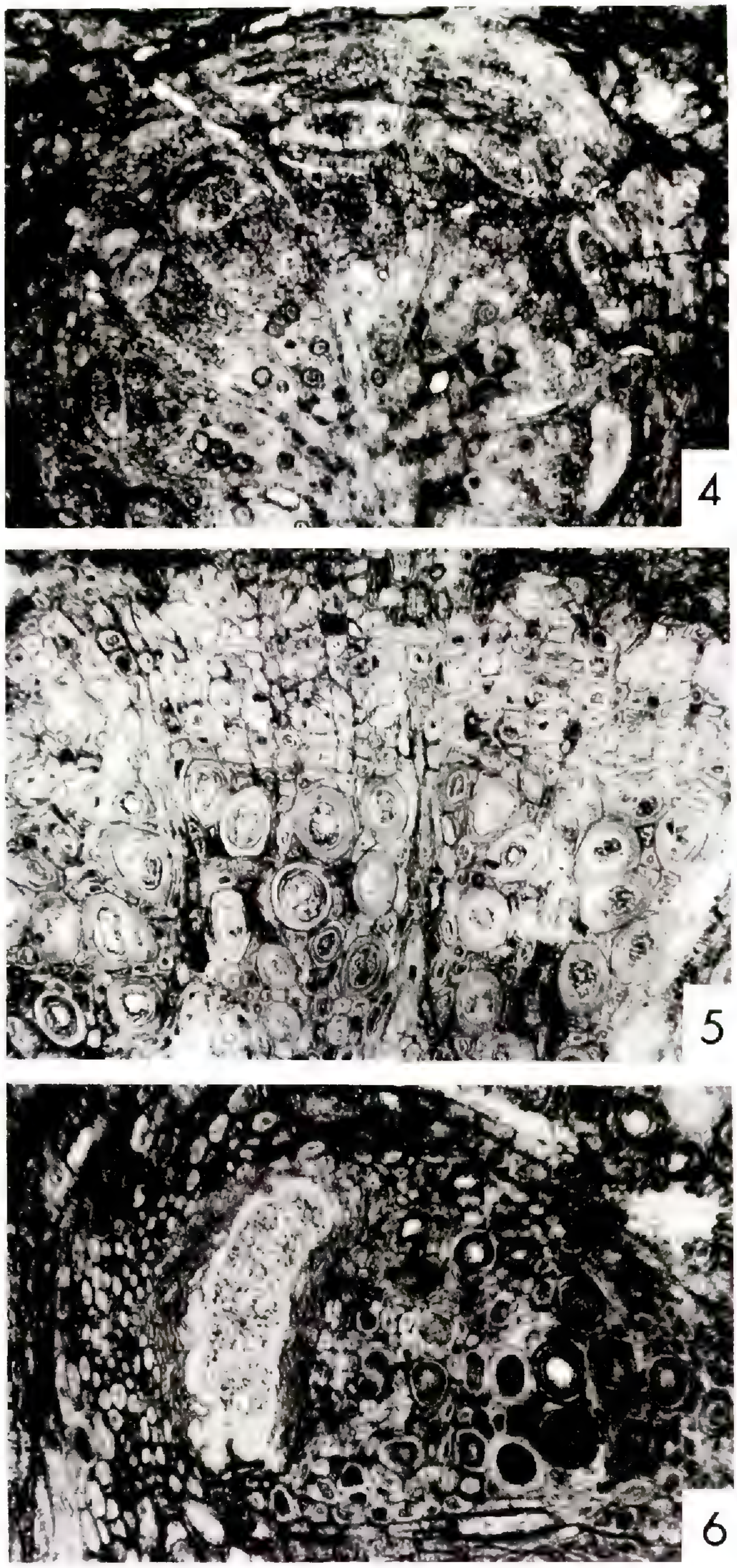
while others have terminal bulges. In some cases, a mass of sclereids, as seen in transverse section, lies in close proximity to a protoxylem point of a vascular bundle and extends into the interfascicular region. Individual sclereids within these masses are often elongated and lie parallel to one another (FIGURE 3). They may be as much as 300 μm in length. Although there is evidence of a cambium within the vascular bundles, there is no discernible sign of an interfascicular cambium. Metaxylem vessels are by far the most conspicuous components of these bundles. The cells are comparatively large in diameter, averaging 45 μm (range, 36–51) radially and 41 μm (28–50) tangentially, but they are less than 300 μm in length. As far as can be observed, thickening of the walls of the conducting cells of the primary xylem is exclusively spiral. It is extremely difficult to interpret the nature of the thickening in the endwalls of the conducting elements in the area of overlap between elements. David Bierhorst examined the thin sections and was able to detect areas in the endwalls

of some of the elements where the spirals were diminished in thickness and resembled bars of scalariform perforations. The nonvascular tissue of the primary xylem is composed of small cells, most of which have thick walls. Some of these cells may be parenchyma, while others appear to be fibers.

Vessels in the secondary xylem are angular, thin walled, and mostly solitary, averaging 53 μm (range, 36–57) in radial and 38 μm (21–54) in tangential diameter. The length of the vessel elements is almost impossible to measure because cell outlines are very faint; also, since the vascular bundles are seldom oriented parallel to the plane of section, few well-defined and undistorted elements can be observed. The vessel elements are, therefore, merely estimated to be about 260–360 μm long. Intervessel pits, in the few places where they can be observed, are small and opposite. Perforation plates are scalariform, with up to 20 but usually less than 10 bars. Parenchyma is sparse and occurs as single cells associated with vessels. Pits in the walls of parenchyma cells are large and lenticular. Medullary rays are heterocellular and 2 or 3 cells wide. Rays within vascular bundles are uniseriate. Thick-walled fibers with slitlike apertures make up the remainder of the nonvascular tissue. A large cavity surrounded by crushed cells occupies the presumed position of the phloem. Each bundle is capped by a group of narrow fibers.

Within the ring of numerous stelar bundles in a transverse section, as many as 15 are much enlarged. Various stages of lateral expansion of the bundles—apparently a result of radial division—can be observed. The larger of these complexes comprise several segments of primary xylem, secondary xylem, and phloem and are separated from their neighbors by bi- or triseriate rays. The enlarged bundles are displaced outwardly into the cortex, and the position they occupied in the stele is filled with parenchyma. The ground tissue of the cortex is composed of large, relatively thick-walled parenchyma cells. Nests of sclereids and large, isolated cells like those in the periphery of the pith are scattered throughout. Most conspicuous and crowded within the cortex are tight circles of vascular bundles; these are as large as 2 mm in diameter and include up to 16 bundles (FIGURE 4). Individual bundles vary in size. Most contain both primary tissue and small cells in radial files in the position of a cambium and/or undifferentiated cambial products (FIGURE 5). Radially aligned cells are absent in smaller bundles. Except in a few cases, large cavities remain in the presumed position of the phloem (FIGURE 6). Each bundle is capped by a group of narrow fibers, and each circle of bundles appears to be bounded by a sheath of flattened cells. Possibly these latter cells were flattened by pressure exerted by centrifugal expansion of the vascular bundles. In some instances the circular arrangement is disrupted, particularly toward the outer edge of the sections. Examination of a series of four transverse sections shows that some of the bundles of a partially disrupted circle remain associated, but that others are twisting away. Fragments of bundles traverse the outer edge of the sections both vertically and horizontally. The arrangement of vascular traces in the cortex appears to be unique, for a search through the literature failed to reveal evidence of similar circles of bundles in the cortex of any structures of either monocotyledons or dicotyledons. I must point out, however, that complete anatomical studies of axes of the primary body of woody plants are very limited;





FIGURES 2–6. **Loishoglia bettencourtii**: 2, nests of sclereids, transverse section, showing convoluted pattern, × 100; 3, pith sclereids, longitudinal section, showing elongated form, × 100; 4, circle of cortical bundles, transverse section, × 37; 5, enlargement of portion of 3 contiguous cortical bundles, transverse section, showing undifferentiated secondary xylem above and primary xylem with thick-walled vessels below, × 100; 6,

studies of inflorescence axes of both woody and herbaceous plants are even more limited.

SYSTEMATIC DESCRIPTION

Loishoglia Page, gen. nov.

Axes with central cylinder of collateral bundles surrounding a pith composed of parenchyma, nests of sclereids, and isolated secretory cells, and a cortex with narrowly wedge-shaped vascular bundles arranged in numerous tight circles of up to 16 bundles per circle. Metaxylem vessels with walls spirally thickened, perforations scalariform. Vessels of secondary xylem solitary with small, opposite intervessel pits. Perforations scalariform with up to 20 but usually fewer than 10 bars. Medullary rays heterocellular, 2 or 3 cells wide.

TYPE SPECIES. *Loishoglia bettencourtii* Page.

Loishoglia bettencourtii Page, sp. nov.

Pith. 1.5 cm in diameter. Parenchyma cells large, thin walled except for peripheral zone of small, thick-walled cells. Secretory cells avg. 102 μm in diameter. Sclereids in lenticular plates 1 cm long and 0.5 cm thick in longitudinal section.

Vascular bundles. Vascular bundles numerous. Primary xylem vessels solitary, isodiametric, avg. 45 μm (range, 32–50) in diameter, ca. 300 μm long. Perforations scalariform. Secondary xylem vessels mostly solitary, avg. 53 μm (36–57) in radial diameter, 38 μm (21–54) in tangential diameter. Vessel element length ca. 360 μm. Intervessel pits small, opposite. Perforations scalariform, with up to 20 but usually fewer than 10 bars. Parenchyma sparse, occurring as single cells associated with vessels. Medullary rays 2 or 3 cells wide, heterocellular; rays within bundles uniseriate. Ground tissue of thick-walled fibers with slitlike apertures. Phloem fibers thick-walled, narrow, forming centrifugal cap as viewed in transverse section, sieve cells not preserved.

Cortex. Circles of vascular bundles numerous; individual bundles similar to those of central stele except secondary tissues undeveloped or lacking. Solitary bundles numerous at periphery. Ground tissue parenchymatous with numerous nests of sclereids. Secretory cells abundant.

MATERIAL. One calcified petrifaction measuring 3.5 cm in diameter and 3 cm in length.

HOLOTYPE. California Academy of Sciences Geological Collections no. 61208.

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individual vascular bundle, transverse section, showing primary xylem to right and cap of phloem fibers to left of large phloem cavity (note crushed cells surrounding cavity), × 70.

The genus is named after Lois Hogle in recognition of her kindness in providing transportation to the collection site. The specific epithet is in honor of the Bettencourt family of Crow's Landing, California, for allowing me to collect on their property over the years.

LOCALITY. Moreno formation. Black Gulch; NE¼, SE¼ sect. 32, R7E, T5S, Oristimba 15″ quadrangle, California.

AGE. Maastrichtian.

DISCUSSION

The specimen remained an enigma for a long time mainly because of the unusual structure of the cortex and the difficulty in determining the nature of the endwalls of the vessel elements in both the primary and the secondary xylem. The presence of a fascicular cambium is an indication that the specimen is a dicotyledon, for in monocotyledons the cambium is exclusively extrafascicular. The anatomy of the stele has characteristics of certain dicot stems. The numerous gaps left by traces in various stages of departure from the stele are suggestive of a system of much-telescoped internodes and possibly a spiral phyllotaxy such as one would expect to find either in the receptacle of a flower with numerous parts or in the peduncle of an inflorescence.

Among flowers examined, receptacles of members of the Magnoliaceae (particularly in the perianth region in *Magnolia* L. and *Liriodendron* L.) proved anatomically most similar to the fossil. In plants of both *Magnolia* and *Liriodendron*, numerous collateral bundles surround a large pith containing nests of sclereids and secretory cells. Cambial activity is minimal and confined to the vascular bundles. Sclereids and secretory cells occur in the stems of many genera of dicots, but the combined occurrence of nests of sclereids of the type observed in *Loishoglia* and secretory cells in both pith and cortex is not common and, as far as I can determine, has been reported only in certain families of the Magnoliales. Among these families, vessel elements of the type observed in the secondary xylem of the fossil are found only in genera of the Magnoliaceae. Although much larger than the secretory cells of the species of *Magnolia*, *Michelia* L., and *Liriodendron* examined, the enlarged cells of parenchymatous tissues in *Loishoglia* may be homologous with them, for they are similar in shape and distribution. In the modern forms examined these cells usually are not surrounded by flattened parenchyma cells as they are in the fossil. It is possible that the condition in the fossil is due to excessive expansion of the secretory cells early in differentiation. Although of the same general type as those in the Magnoliaceae, sclereids in *Loishoglia* tend to be much longer. The structure of the vascular elements in the fossil is consistent with that in many members of the Magnoliaceae. Scalariform perforations with less than ten bars are characteristic of vessels in the secondary xylem, and opposite intervessel pits are present in a number of genera. Vessel elements of the primary xylem range from slightly over 200 μm to 500 μm in length in the stalk and receptacle of the magnolia flowers examined. Because of poor preservation, it was impossible to measure more than one vessel in the primary xylem of the fossil.

This element, which was 290 μm long, falls in the lower portion of the range observed in *Magnolia*. However, the numerous fragments visible in longitudinal sections indicated that the average length of vessel elements was probably greater than 290 μm. The most obvious difference between the fossil and the modern forms lies in the cortex. Most of the cortical bundles in the receptacle of *Magnolia* or *Liriodendron* are single or in pairs, but occasionally a circle of three (or rarely four) occurs, particularly in *Liriodendron*. In the specimens examined (*L. tulipifera* L. and ornamental varieties of *M. grandiflora* L.) cortical bundles occurring in circles are broadly wedge shaped and arranged (as in the fossil) so that in transverse section the apices of the wedges are in juxtaposition. Parenchyma cells immediately surrounding a circle of bundles differ only slightly in shape and size, so there is nothing resembling the sheaths of flattened cells characteristic of the circles of bundles in the fossil.

If the fossil is homologous with floral axes of members of the Magnoliaceae, an explanation of the pattern of cortical traces is necessary. Two interpretations are possible. First, the specimen may represent a portion of the axis of an individual flower, and the cortical bundles traces to its various components. As noted above, occasional circles of three or four wedge-shaped vascular bundles occur in transverse sections of flower stalks and receptacles of *Magnolia* and *Liriodendron*. It is probable that these circles represent situations in which branches of traces developed parallel to one another for a short distance before diverging from the parent trace. Although more complex, the condition in the fossil may be similarly explained. The seeming complexity may stem from the more profuse branching of traces in the fossil. In sections of receptacles of *Liriodendron* and *Magnolia*, many traces diverging from the stele appear to be dividing bilaterally. In the fossil some stelar bundles appear to be dividing bilaterally, but others look as though they were undergoing multiple divisions (see FIGURE 1). Whereas in the modern forms these branches soon diverge, in the fossil most remain associated for at least the length of the specimen, and some are joined by a sympodium from another level of the stele. (Since the direction of provascular development is not known, trace patterns are discussed here as if they had been basipetal.)

The second interpretation, derived from Nast's (1944) description of the vasculature of the cymelike inflorescences in species of *Drimys* J. R. & G. Forster (Winteraceae), is that the specimen may have been part of the peduncle of a compound inflorescence, in which case the circles of bundles may be traces to pedicels. Nast (p. 458) stated that in the flowering stalk, "each thickened area of the stele breaks up into a number of bundles as it leaves the central cylinder and almost immediately assembles into steles of the floral pedicels. The pedicels may contain one or two concentric bundles or a cylinder of bundles." The cortical circles of bundles in the fossil, *Loishoglia*, may be homologous with the pedicel traces of *Drimys*; however, unlike the latter, which enter the pedicels at more or less the same level in the axis as they depart from the central stele, those in the fossil continued on at a much more acute angle for some distance before connecting with a pedicel. That groups of traces may have maintained a circular configuration on departure from the main axis is suggested by the presence of circles in longitudinal sections tangential to the

outermost edge of the specimen. More difficult to explain in either interpretation are the numerous individual bundles and small circles crowded at the outer edge of the cortex in transverse sections. In these bundles the cells are crushed and wrinkled as if atrophied.

Although *Loishoglia* has several anatomical characteristics in common with the Magnoliaceae, the unique vascular pattern of the cortex distinguishes it from all members of both that family and related ones. If the circles of bundles in the cortex represent incipient steles of pedicels, this would suggest that the inflorescence was complex. Although flowers of the Magnoliaceae are generally solitary, in *Elmerrillia* Dandy and *Michelia* there may be more than one per inflorescence. Moreover, there is some evidence that the flowering axes of the closest relatives of the Magnoliaceae, the Degeneriaceae and Himantandraceae, may be reduced from more complex structures. In *Galbulimima* F. M. Bailey (Himantandraceae) bracts at the base of the receptacle subtend axillary buds that occasionally develop into subsidiary flowering axes (Bailey *et al.*, 1943). The flowering axes of *Degeneria* I. W. Bailey & A. C. Sm. bear bracteoles thought by Bailey and Smith (1942) to indicate that the axes had been reduced from more complicated systems. Compound inflorescences, therefore, may have been characteristic of the ancestral group from which these families were derived.

Three wood and stem specimens showing possible affinities with the Magnoliaceae or related families have previously been described from the Maastrichtian of central California. Two of these (SUPTC[1] 10,000, *Magnoliaceoxylon panochensis* (Page) Wheeler, Scott, & Barghoorn (Page, 1970), and CASG 60425 (Page, 1980)) are fragments of secondary wood, and one (CASG 60133 (Page, 1980)) is a young stem with pith and both primary and secondary xylem. The possible relationship between the latter specimen and the Magnoliaceae was not recognized initially because its solitary pores and heterocellular rays are not typical of the family. It does, however, contain pith sclereids of the magnoliaceous type, and secretory cells are present in the rays and pith. Of the three specimens, 60133 is most similar anatomically to *Loishoglia*. It is a stem or branch 2.5 cm in diameter with a large pith 1 cm in diameter. Pores in the metaxylem are 21–43 μm in diameter; those in the secondary xylem 86–96 μm. Intervessel pits in the secondary xylem are small and opposite, and perforation plates are scalariform with less than ten bars. Secretory cells in the pith are devoid of contents and difficult to distinguish in transverse section from the very large, thin-walled parenchyma cells, but a few can be observed in the longitudinal plane where the parenchyma cells are mostly flattened. The secretory cells are comparable in size to those in *Magnolia* (avg. 80 μm) and are thus smaller than those observed in *Loishoglia*. Enlarged cells in the rays, interpreted as secretory (Page, 1980, *fig. 4*), are closely similar to such cells in the rays of secondary xylem in *Magnolia*. Pith sclereids are much like those in *Loishoglia*. An additional feature typical of the Magnoliaceae can be observed in transverse sections of specimen 60133. The sections are through a

[1]Stanford University Paleontological Type Collection, now housed at the California Academy of Sciences, San Francisco.

multilacunar node with a large median trace flanked by two small traces and eight additional lateral traces. As described by Canright (1955), the typical nodal pattern in *Magnolia* is similar except for the presence of a stipular trace opposite the median trace. Tissues in the area where a stipular trace would be expected were not preserved in the fossil; therefore, it is not possible to determine whether such a trace was originally present. Several traces are present in the fossil that are not figured in Canright's diagram. This difference may not be significant, for he has pointed out that the number of nodal traces in species of *Magnolia* is extremely variable both inter- and intraspecifically; however, although the number of lateral traces may vary from four to fifteen, the median and stipular traces are always present.

The numerous anatomical similarities observed in CASG 60133, *Loishoglia,* and stems of the Magnoliaceae suggest that the fossils were related to one another and to the Magnoliaceae. Although vessel elements in the secondary xylem of *Loishoglia* are on the average smaller in diameter than those in either 60133 or most members of the Magnoliaceae, they compare well in size with elements in the earliest-formed secondary xylem (where the vessels are about half the diameter of those in subsequent increments). Secretory cells in *Loishoglia,* however, are much larger than those in 60133 and the species of *Magnolia, Michelia,* and *Liriodendron* examined. It is possible that the two fossils were related but not necessarily derived from members of the same natural species or genus. The locality from which 60133 was collected is slightly younger than the horizon in which *Loishoglia* was found. It has been estimated (Page, 1981) that the two localities are separated by an interval of about 1.5 million years.

The two specimens of secondary wood, SUPTC 10,000 (from the same locality as *Loishoglia*) and CASG 60425 (from the same locality as 60133), are closely similar to the woods of the modern Magnoliaceae except for the absence of terminal parenchyma. They differ from each other in that the intervessel pits appear to be scalariform in 60425, whereas they are mostly opposite in 10,000. Neither specimen shows evidence of secretory cells, and since both consist only of secondary wood, no sclereids are present. Until additional material becomes available, it is useless to speculate on the relationship between these two specimens and *Loishoglia.* The lack of secretory cells in itself may not be significant; among modern species of Magnoliaceae it is not unusual for such cells to be absent from the secondary wood but consistently present in primary tissues.

The magnolialian complex can be traced at least to the early part of the Upper Cretaceous, as indicated by fruits and leaves described by Dilcher *et al.* (1976), Crane and Dilcher (1982), and Dilcher and Crane (1982, 1984) from the early Cenomanian of Kansas. When compared with modern derivatives of the ancestral complex, *Loishoglia* appears to be most closely allied to the clade consisting of the Degeneriaceae, Magnoliaceae, and Himantandraceae. *Loishoglia* and the putative magnolioid wood specimen (CASG 60133) can be added to a growing list of extinct Cretaceous genera of dicotyledons. The knowledge that a significant number of Cretaceous angiosperm genera are now extinct should be sufficient reason for caution in assessing the degree of relationship between pre-Tertiary woods and supposed modern counterparts.

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SYSTEMATICS AND PALYNOLOGY OF PICRODENDRON: FURTHER EVIDENCE FOR RELATIONSHIP WITH THE OLDFIELDIOIDEAE (EUPHORBIACEAE)

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C. R. Broome, and G. L. Webster

Although known to botanical science for 285 years, the genus *Picrodendron* Planchon has been poorly understood for most of this time. The most pervasive problem has been that of discerning familial relationships, and there have been additional difficulties in typifying the generic name (Hayden & Reveal, 1980) and in distinguishing its three nominate species. This paper provides a systematic treatment for *Picrodendron* and demonstrates its relationships with Euphorbiaceae subfam. Oldfieldioideae Köhler & Webster as evidenced by data on gross morphology, palynology, anatomy, and cytology.

Picrodendron captured the attention of Dr. William T. Gillis while he was pursuing floristic studies of the Bahama Islands. During the decade preceding his death, Gillis accumulated a considerable amount of information on this problematic genus; he was attempting to complete this long-standing project in the weeks before he died in June, 1979. It has been a privilege tempered with sadness for one of us (W. J. H.) to prepare this paper from Gillis's notes and the contributions that he had solicited from the other authors. Herbarium and field studies reported here were performed by Gillis and form the basis for much of what appears in the generic description and the sections on biogeography and economic uses; taxonomic judgment at the species level is also Gillis's. Broome and Stone contributed descriptions of pollen and most of the discussion concerning the Juglandaceae; information on relationships with the Euphorbiaceae was provided by Webster.

This paper is a tribute and memorial to Gillis, an indefatigable student of the Bahama flora.

MATERIALS AND METHODS

Taxonomic treatment of *Picrodendron* is based on examination of numerous specimens in the wild, in cultivation, and in the herbarium. Herbarium specimens examined are listed in the Appendix.

Pollen descriptions are based upon examination of the following specimens. *Austrobuxus carunculatus* (Baillon) Airy Shaw: New Caledonia, Quinne-Tal, *Stauffer & Blanchon 5751* (DUKE); New Caledonia, Kouébuni, *Hürlimann 571* (US). *Austrobuxus eugeniifolius* (Guillaumin) Airy Shaw: New Caledonia, *Guil-*

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laumin & Baumann-Bodenheim 12908 (US). *Mischodon zeylanicus* Thwaites: Sri Lanka, *De Silva 28* (US). *Oldfieldia africana* Bentham & Hooker f.: Ivory Coast, *Voorhoeve 1963* (MO). *Picrodendron baccatum* (L.) Krug & Urban: Cuba, Santiago, *Clemente 6587* (GH, US); Jamaica, *Harris 12516* (US). *Piranhea longepedunculata* Jablonski: Venezuela, *Blanco 299* (US). *Tetracoccus dioicus* Parry: United States, California, *Munz 12614* (MO). *Tetracoccus hallii* Brandegee: United States, California, *Dressler 1211* (MO); Arizona, *Kearney & Harrison 7530* (US).

For brightfield microscopy, dried pollen was acetolyzed, treated with potassium hydroxide, and mounted in glycerine jelly. Since the pollen grains were nearly spherical, diameter measurements were made without regard to the polar axis; a minimum of 30 grains were measured at × 1000 with a × 40 high dry objective and × 25 oculars. Photomicrographs of acetolyzed grains were taken with a × 90 oil immersion apochromatic objective (n.a. 1.32) and a × 10 negative ocular at × 1500 on Kodak Ortho or Pan sheet film, or at × 370 on Kodak 35 mm High Contrast Copy film. For SEM observations, acetolyzed pollen grains were air dried from 70% ethanol and then coated with gold-palladium (60:40) in a vacuum evaporator. For TEM, dried pollen was fixed for 10–12 hours in 2% glutaraldehyde buffered with 0.1 M Sørensen's phosphate buffer at pH 7.0, washed, and finally postfixed for 2 hours in 2% phosphate-buffered osmium tetroxide. Immediately after stepwise dehydration in ethanol, the pollen was embedded in Spurr resin, standard formulation. Thin sections were poststained either in aqueous potassium permanganate solution or in a uranyl acetate–lead citrate combination.

Observations of seedling morphology in *Picrodendron* were obtained from greenhouse-grown seedlings at the University of Richmond, Richmond, Virginia. The seeds came from plants cultivated at the Fairchild Tropical Garden and originally collected from Driggs Hill, South Andros, Bahama Islands. Voucher specimens for these plants are *Gillis 10924, 10975,* and *11031* (AAH, FTG, IJ).

TAXONOMIC HISTORY

A century and a half elapsed between the first published record of *Picrodendron* by Sloane (1696) as "*Nux juglans trifolia. . .*" and its ultimate recognition as a distinct genus (Planchon, 1846). It is not surprising, perhaps, that colonial Europeans, overwhelmed by the novelty and diversity of the neotropical flora, associated this plant with the familiar walnut, since there are certain gross resemblances. Consider, for example, the much-quoted but uncritical passage from Browne (1756) describing the "Jamaica walnut": "The outward part of the fruit is soft and pulpy, when ripe; but the hard ligneous shell, and the partitions and lobes of the seed, as well as parts of the flower, agree perfectly with the general characteristics of the genus." Linnaeus apparently saw neither living nor herbarium specimens of *Picrodendron,* which he nevertheless named *Juglans baccata* (Linnaeus, 1759), referring to Browne (1756), who had in turn referred to Sloane's (1725) illustration (see FIGURE 1). Amazingly, this link with the Juglandaceae has persisted for over two and a half centuries despite

FIGURE 1. Lectotype of *Picrodendron baccatum* (reproduced from H. Sloane, A Voyage to the Islands Madera, Barbados, Nieves, S. Christophers and Jamaica **2:** *t. 157, fig. 1.* 1725).

having been based on very superficial analyses and a decidedly nondefinitive illustration.

Besides being considered a walnut, *Picrodendron* has also been treated as *Tapia* (i.e., *Crateva* L.) (Capparaceae), by Catesby (1734); *Schmidelia* (i.e., *Allophylus* L.) (Sapindaceae), by Richard (1845); and *Rhus* (Anacardiaceae) by Macfadyen (1837). Actually, Macfadyen had misapplied De Candolle's (1825) name *Rhus arborea* (basionym: *Toxicodendron arboreum* Miller). The names of Miller and De Candolle apply to *Allophylus,* but Macfadyen's specimen unmistakably represents what is now known as *Picrodendron.* Macfadyen's error unfortunately threw the application of Planchon's (1846) name *Picrodendron* into uncertainty, for Planchon based the genus on both an authentic Macfadyen specimen (κ!) and the basionym *Rhus arborea* DC. Planchon's species name, *P. arboreum,* is therefore a synonym of *Allophylus* L. Prior to the Sydney Congress of 1981, however, the Code of Botanical Nomenclature was unclear whether, in such a situation, the name *Picrodendron* should be typified by the species represented in the literature citation (i.e., *Rhus arborea*/*Allophylus*) or by the species represented by the specimen cited (i.e., *Macfadyen s.n.*). Consequently, Hayden and Reveal (1980) proposed to conserve *Picrodendron* from the 1859 publication of Grisebach; full particulars can be found in that paper. However, revisions incorporated into the Code at Sydney (see Taxon **30:** 103–105, 200–207, 904–911) now permit a different course. New Article 10.4 states, "By conservation, the type of the name of a genus can be a specimen used by the author in the preparation of the protologue, other than the type of a name of an included species." Further, new Article 14.8 reads, "A name may be conserved with a different type from that designated by the author or determined by application of the Code." Thus, we herein retain Planchon's name, to be typified, by conservation, by Macfadyen's specimen of *Picrodendron baccatum.*

Picrodendron has been treated variously as a single species or as two or three insular endemics. Grisebach (1859) realized that the Jamaican *Juglans baccata* L. and *Picrodendron arboreum* Planchon were conspecific with the Cuban *Schmidelia macrocarpa* A. Rich. Grisebach called these plants *Picrodendron juglans,* a superfluous name that was also applied to plants from the Bahamas (Gardiner & Brace, 1889). Urban (1893) restored Linnaeus's epithet, forming *Picrodendron baccatum* (L.) Krug & Urban for Jamaican and Cuban elements, but distinguished Bahamian material as var. *bahamense* Krug & Urban. Britton (1906) preferred to treat Cuban and Bahamian elements as one species, *P. macrocarpum* (A. Rich.) Britton.

Small (1917) distinguished plants from Hispaniola as a third species, *Picrodendron medium* Small, and his concepts of the three species can be summarized as follows: *P. baccatum* from Jamaica, characterized by dark leaflets with acute apices, long fruiting pedicels, and spherical fruits with thin endocarp; *P. macrocarpum* from Cuba and the Bahamas, characterized by blunt, pale leaflets, short fruiting pedicels, and somewhat ovoid fruits with thick endocarp; and *P. medium* from Hispaniola, characterized by leaflets similar to those of *P. baccatum,* and endocarp similar to that of *P. macrocarpum.* Small's distinctions seem trivial; moreover, these three epithets have been used frequently in senses

other than those outlined by Small (Gómez de la Maza & Roig y Mesa, 1916; Urban, 1920; Barker & Dardeau, 1930; Moscoso, 1943; Howard, 1955; Adams, 1972).

As noted above, early concepts of the relationships of *Picrodendron* varied widely, and disparate taxonomic associations have persisted throughout most of its subsequent history. Varying opinions regarding its relationships include placement in or association with the Simaroubaceae (Planchon, 1846; Bentham & Hooker, 1862; Urban, 1920; Barker & Dardeau, 1930; Moscoso, 1943), Juglandaceae (Grisebach, 1859), Burseraceae (Grisebach, 1866), Terebinthaceae (Hallier, 1908), Picrodendraceae (Small, 1917, and numerous recent authors), Euphorbiaceae (Fawcett & Rendle, 1917; Thorne, 1976; Webster, 1975; Takhtajan, 1980; Cronquist, 1981), and Bombacaceae (Hallier, 1921). The family Picrodendraceae has been assigned to the Juglandales (Cronquist, 1968; Hutchinson, 1973), Rutales (Scholz, 1964; Takhtajan, 1966), and Euphorbiales (Novák, 1961; Takhtajan, 1969; Airy Shaw, 1973; Cronquist, 1978).

ECONOMIC IMPORTANCE

There are several recorded uses of *Picrodendron*, all of minor economic consequence. In Hispaniola the plants are commonly grown as a windbreak. In Jamaica the fruits are occasionally eaten, although Fawcett and Rendle (1920) stated that this should be done with caution. León and Alain (1951) reported that the leaves are eaten by animals. Curiously, one of its common names in the Dominican Republic, "mata becerro," means "calf killer." Jiménez (pers. comm.) reported that in the Dominican Republic leaves of *Picrodendron* are reduced to powder and used to kill bedbugs and lice. Sawyer (1955) reported that on Great Inagua a tea made from the leaves is used in the treatment of poisoning from eating fish; additional medicinal uses were reported in Roig y Mesa (1945). The viscid exocarps of *Picrodendron* fruits have been employed for their saponin in washing clothes. Record and Hess (1943) mentioned that the wood, which finishes smoothly and is resistant to decay, has been used in naval construction and turnery.

SYSTEMATIC TREATMENT

Picrodendron Planchon, London J. Bot. **5:** 579. 1846, nom. cons. prop. TYPE: "Jamaicae, Mac Fadyen, in herb. Hook.," typ. cons. [*Juglans baccata* L. = *P. baccatum* (L.) Krug & Urban].

Tree to 12 m, dioecious (rarely monoecious); bark rough, bitter to taste, gray, furrowed to shaggy in age; shoots finely pubescent. Leaves alternate, palmately trifoliolate, 1–2 dm long, deciduous prior to flowering; stipules inconspicuous, early deciduous; petioles 4–10 cm long, minutely pubescent; leaflets with the petiolules 0.5–2.5 cm long, joined at base, the blades 1.5–11 cm long, elliptic, oblong, ovate, or obovate, obtuse to emarginate apically, unequal basally on lateral leaflets, otherwise symmetrical, pinnately veined, finely reticulate, with the upper surface glabrous to glabrate and occasionally with tiny hairs proximally on midvein, the lower surface slightly paler green than the upper, glabrate

to puberulent but densely pubescent on major veins. Flowering first during third year. Staminate flowers in stalked, puberulent catkins borne in axils of leaves of previous season's growth, appearing before or with leaves in compressed heads, elongating to loosely clustered spikes; flowers greenish yellow, subtended by (1 to) 3 (to 7) bracts, these imbricate, to 1.5 mm long, with central one larger and overlapping laterals, acute, deltoid; perianth absent; stamens 3 to 54, on convex hemispherical receptacle, the filaments free, shorter than anthers (less than 0.5 mm), short-subulate, glabrous, the anthers 2-celled, basifixed, to 1.5 mm long, oval, notched at apex and cordate at base, sparingly puberulent especially at tip, dehiscing longitudinally when mature, slightly extrorse; pollen spinose-verrucate, 5- to 8-porate; pistil absent. Pistillate flowers axillary, borne singly on shoots of current season; pedicels 2–4 cm long, abruptly widened below the finely pubescent, concave receptacle; flowers green, subtended by 4 or 5 valvate bracts, these ascending-recurvate, sepaloid, ± unequal, 2.5–8 mm long, lanceolate, gland bearing, remotely toothed or ciliate; staminodes absent; ovary superior, sessile, ovoid, 2-carpellate, naked; the style terminal, slightly longer than ovary, columnar, the stigmas 2, divergent, longer than style, stout-subulate, with revolute margins; ovules 2 per locule, pendulous from central axis, anatropous, the raphe ventral, the integuments 2, the obturator cushionlike, reddish brown, attached to placenta above ovules, covering micropyles, withering in fruit. Fruits smooth, 2-locular, indehiscent, globose to ovoid drupes, 1.5–2.5 cm long, yellow-orange to yellowish green at maturity, nodding, dry black; exocarp thin, fleshy, with numerous vesicles bearing bitter juice; endocarp 1.5–2 mm thick, woody to bony, brittle, marked by 4 equidistant longitudinal lines. Seed(s) 1 (all but 1 ovule usually aborting) (rarely 2, with 1 in each locule), nearly terete to irregularly ovoid; endosperm lacking; testa membranaceous, enclosed between folds of cotyledons; hypocotyl and micropyle superior; epicotyl large, turned back on funicle at right angles to cotyledons; cotyledons plicate, corrugated; nucellus convoluted.

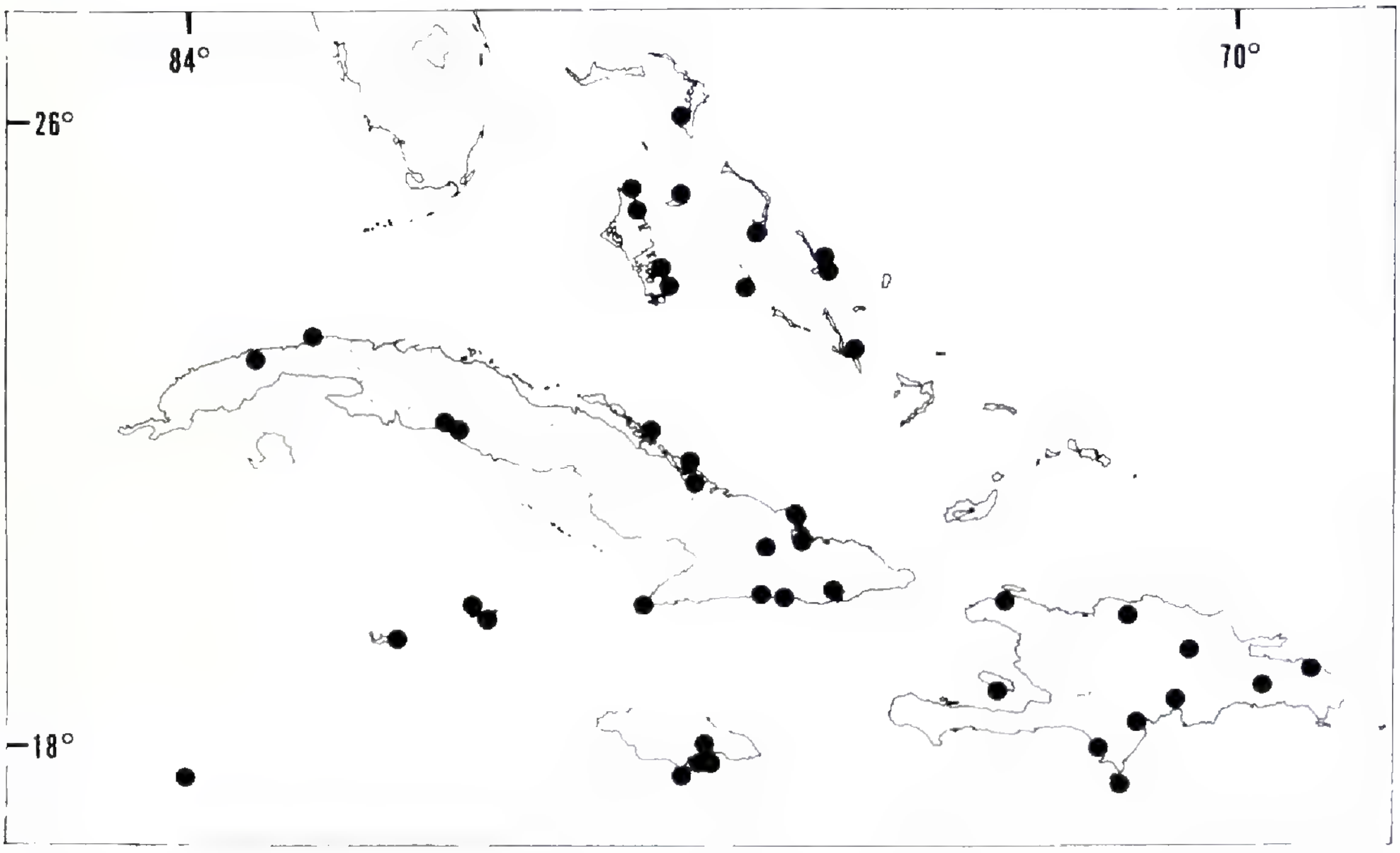
A monotypic neotropical genus found on the Bahama Islands, Cayman Islands, Cuba, Hispaniola, Jamaica, and the Swan Islands (see MAP 1).

Picrodendron baccatum (L.) Krug & Urban, Bot. Jahrb. Syst. **15:** 308. 1893.
Juglans baccata L. Syst. Nat. ed. 10. 1272. 1759. LECTOTYPE: Sloane, Voy. Isl. Madera, Barbados, Nieves, S. Christophers & Jamaica **2:** *t. 157, fig. 1.* 1725. The typotype is in the Sloane Herbarium, H.S. 5: 49 (BM!). *Picrodendron juglans* Griseb. Fl. Brit. W. Indian Is. **2:** 177. 1859, nom. superfl. FIGURE 2.

Schmidelia macrocarpa A. Rich. *in* Sagra, Hist. Phys. Pol. Nat. Cuba **10:** 116. *pl. 30.* 1845. TYPE: Cuba, *Sagra s.n.* (lectotype, P, Herb. Rich.!). *Picrodendron macrocarpum* (A. Rich.) Britton, Bull. New York Bot. Gard. **4:** 139. 1906.

Picrodendron baccatum var. *bahamense* Krug & Urban, Bot. Jahrb. Syst. **15:** 308. 1893. TYPE: Bahama Is., Hog Is. [now Paradise Is., off New Providence], March [?]. *Eggers 4402* (holotype, B, destroyed).

Picrodendron medium Small, Bull. New York Bot. Gard. **18:** 185. 1917. TYPE: Santo Domingo, Prov. Azua, northeast of Azua, 20 March 1913, *Rose et al. 4042* (holotype, NY!; isotype, US!).



MAP 1. Distribution of collections of *Picrodendron* examined (not including cultivated material).

Since examination of herbarium material and of living plants both in cultivation and in the field has failed to uncover any reliable means of separating the three previously distinguished species, we consider the genus to be monotypic, consisting of the somewhat variable *P. baccatum* (L.) Krug & Urban. Other authors (Record & Hess, 1943; Adams, 1972) have expressed doubts about the distinctness of these entities, and monotypic status has been advocated by Gillis (1974) and Correll (pers. comm.).

Although adult phyllotaxy is consistently alternate, the first pair of leaves above the cotyledons on seedlings is opposite. These first true leaves are otherwise similar to later-formed foliage. Of the natural populations of *Picrodendron* studied, all appear to be strictly dioecious. However, one tree cultivated on the estate of Mrs. Alvin R. Jennings in Coral Gables, Florida, is consistently monoecious, producing staminate flowers before pistillate ones. Other trees, presumably from the same introduction, are strictly unisexual (staminate). Thus, this tree appears to be an exceptional individual, not representing any deviant population.

Of 220 herbarium specimens examined, only six were of pistillate material in flower. Pistillate flowers are probably seldom gathered because they generally appear for only a week to ten days each year, usually during the first two weeks in May, and they are green much like the leaves and are therefore inconspicuous.

A profusion of common names suggests that *Picrodendron* is well known to local inhabitants throughout its geographic range. In the Bahamas it is known as blackwood or olive; in the Cayman Islands, black ironwood, cherry, or wild plum; in Cuba, aceituna, gua negro, guayo, llana, llanilla, mangle negro, roblecillo, vanilla-prieta, yana prieta, yanilla, or yanilla-prieta; in the Dominican

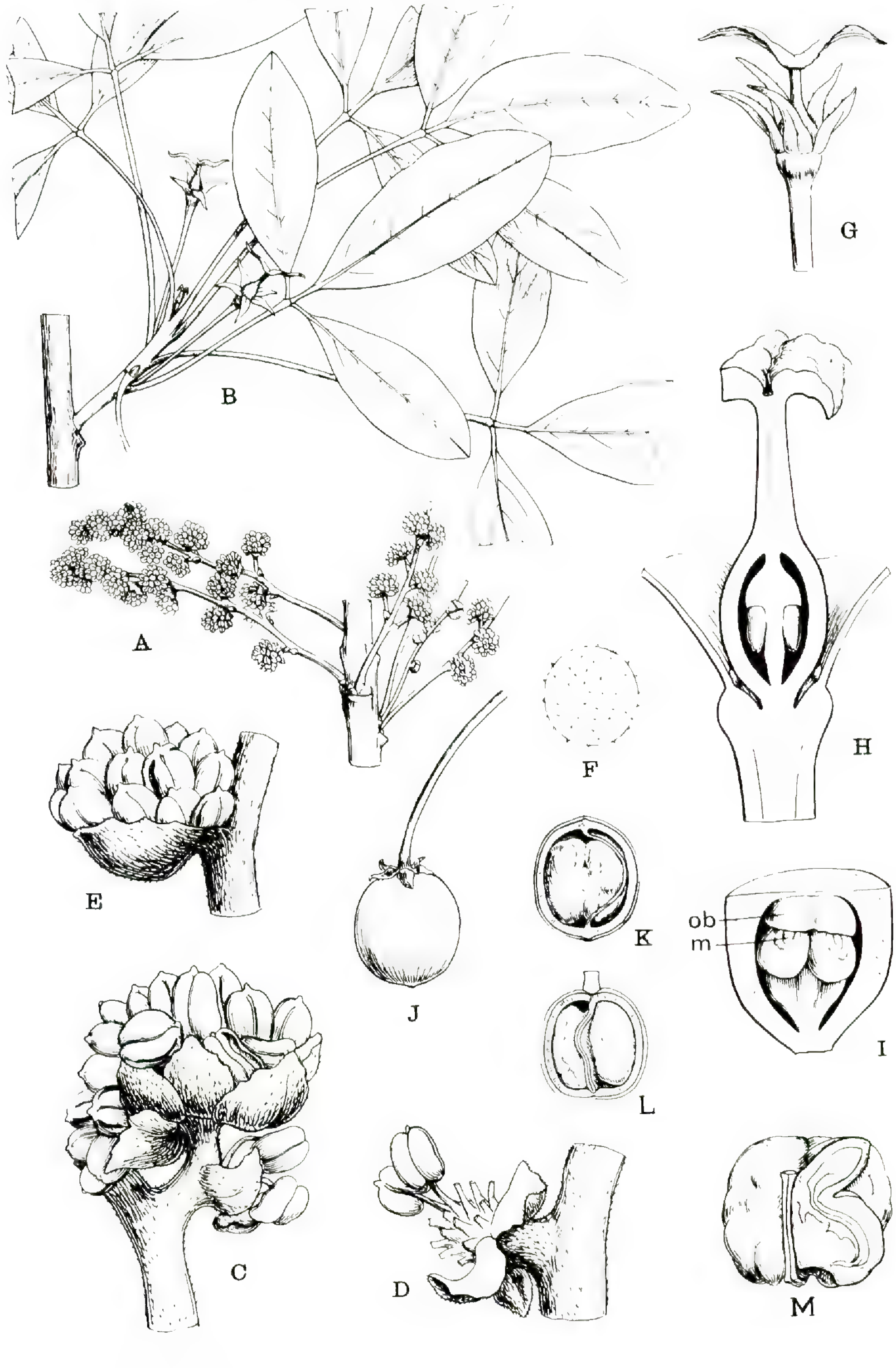


FIGURE 2. *Picrodendron baccatum:* A, twig with staminate inflorescences, × .45; B, twig with pistillate inflorescences, × .45; C–E, staminate flowers, × 8; F, pollen grain, × 460; G, pistillate flower, × 2.3; H, pistillate flower, longitudinal section, showing 2 locules (note glands at base of perianth), × 5.75; I, ovary, longitudinal section, showing

Republic, lemba, manzanilla (manzanillo), or mata becerro; in Haiti, gris-gris noir or simarouba; and in Jamaica, Jamaican walnut or wild plum.

EXCLUDED SPECIES. *Picrodendron arboreum* (Miller) Planchon, London J. Bot. **5:** 579. 1846, based on *Toxicodendron arboreum* Miller, Gard. Dict. ed. 8. *Toxicodendron* no. 8. 1768. TYPE: *Miller s.n.* (BM!). *Rhus arborea* (Miller) DC. Prodr. **2:** 73. 1825, non *R. arborea* Macfad. Fl. Jamaica **1:** 227. 1837 (= *Allophylus cobbe* (L.) Raeuschel, *sensu* Leenhouts, 1967).

BIOGEOGRAPHY AND ECOLOGY

Picrodendron, together with 20 other genera, has a Greater Antillean distribution that omits Puerto Rico (Howard, 1973). *Picrodendron baccatum* is one of several species (e.g., *Catalpa punctata* Griseb., *Pseudocarpidium wrightii* Millsp., *Heliotropium ternatum* Vahl, *Linociera bumelioides* Griseb.) that are found in both the Bahamas and the Greater Antilles.

In the Bahamas, *Picrodendron* grows on the islands situated on the Great and Little Bahama banks. Neither the Great nor the Little Bahama Bank has ever been connected by land to the Greater Antilles. However, during low-water stages of the Pleistocene, the greatly enlarged above-water portion of the Great Bahama Bank extended to within only 25–35 miles of the enlarged Cuban platform, greatly enhancing the chances of dispersal to the Bahamas from Cuba. Even today, the northern fringing Cuban Islands are less than 150 miles from South Andros on the Great Bahama Bank.

The Great and Little Bahama banks are also believed never to have been connected to each other by land. The Northwest Providence Channel, which separates them today, has probably not been less than 20 miles wide during the last million years. Migration from Cuba to the Great Bahama Bank and thence to the Little Bahama Bank is not difficult to postulate. As yet, *Picrodendron* has not moved across the Crooked Island Passage—a very important biogeographical barrier to plant and animal migration—to the islands of the Bahamas or the Turks and Caicos islands to the southeast.

Ecologically, *Picrodendron* is a calciphile that apparently has some degree of salt tolerance. Specimens have often been collected from limestone substrates, either in arid habitats or near the landward margins of mangrove formations. Seifriz (1943) noted that it grows together with mangroves in Cuba, where it is often situated between zones of *Avicennia germinans* (L.) L. and *Laguncularia racemosa* (L.) Gaertner f. Howard (1955) also recorded it on Beata Island, near mangroves and in association with other coastal species such as *Suriana maritima* L., *Thespesia populnea* (L.) Solander ex Corrêa, and

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paired ovules of 1 locule (ob = obturator, m = micropyle), × 11.5; J, fruit, × .75; K, 1-seeded fruit, longitudinal section (note displaced septum), × .45; L, 2-seeded fruit, longitudinal section, × .45; M, seed, sectioned to show radicle and cotyledons, × 1.75. (Reproduced from W. FAWCETT & A. B. RENDLE, Flora of Jamaica **4:** *fig. 90.* 1920, with permission of Trustees of British Museum (Natural History).)

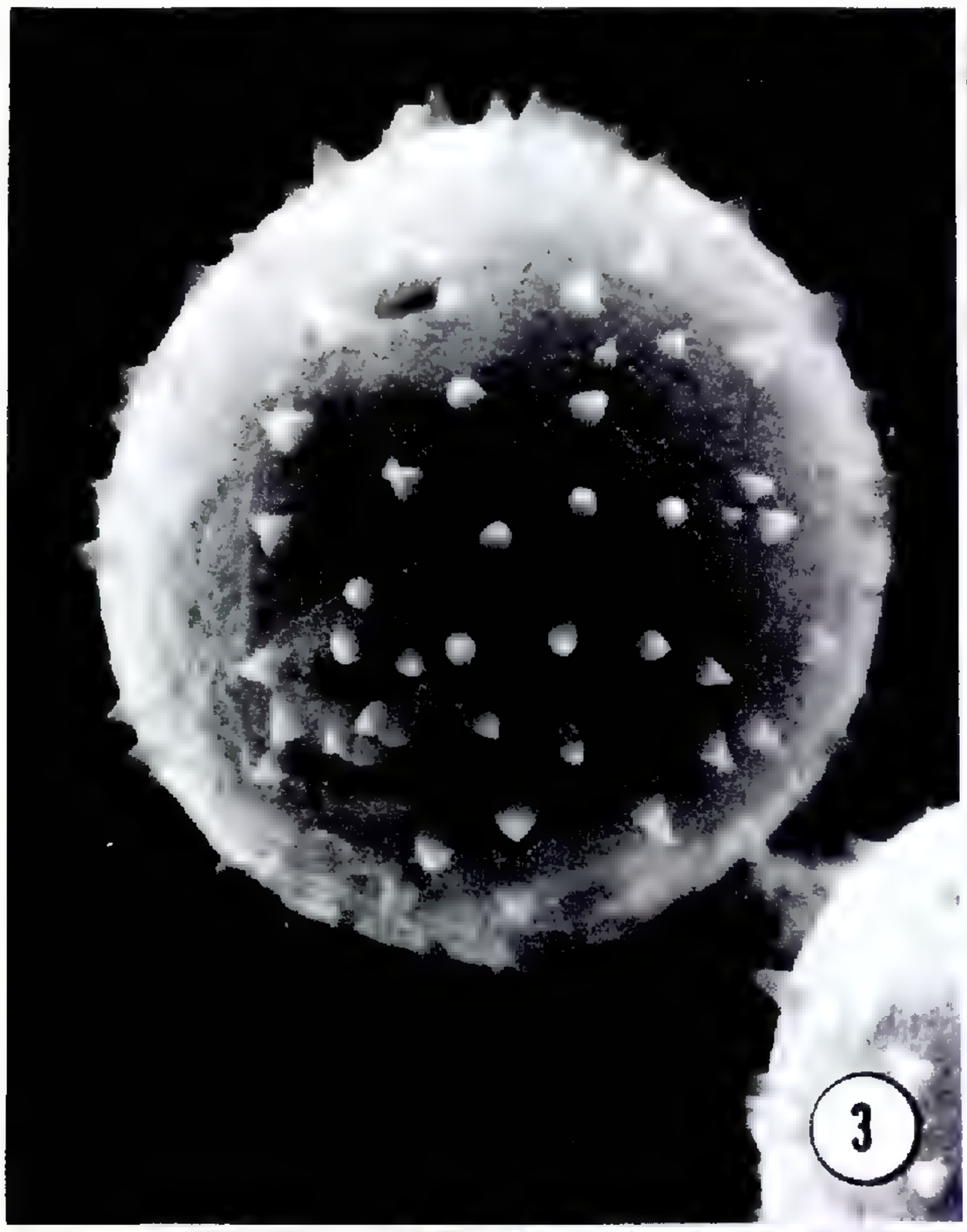
Amyris elemifera L. On the other hand, Asprey and Robbins (1953) included it as a constituent of "dry limestone scrub forests" in Jamaica. Presumably, suitable habitats for *Picrodendron* are widespread in the West Indies; its somewhat restricted geographic distribution is thus all the more interesting.

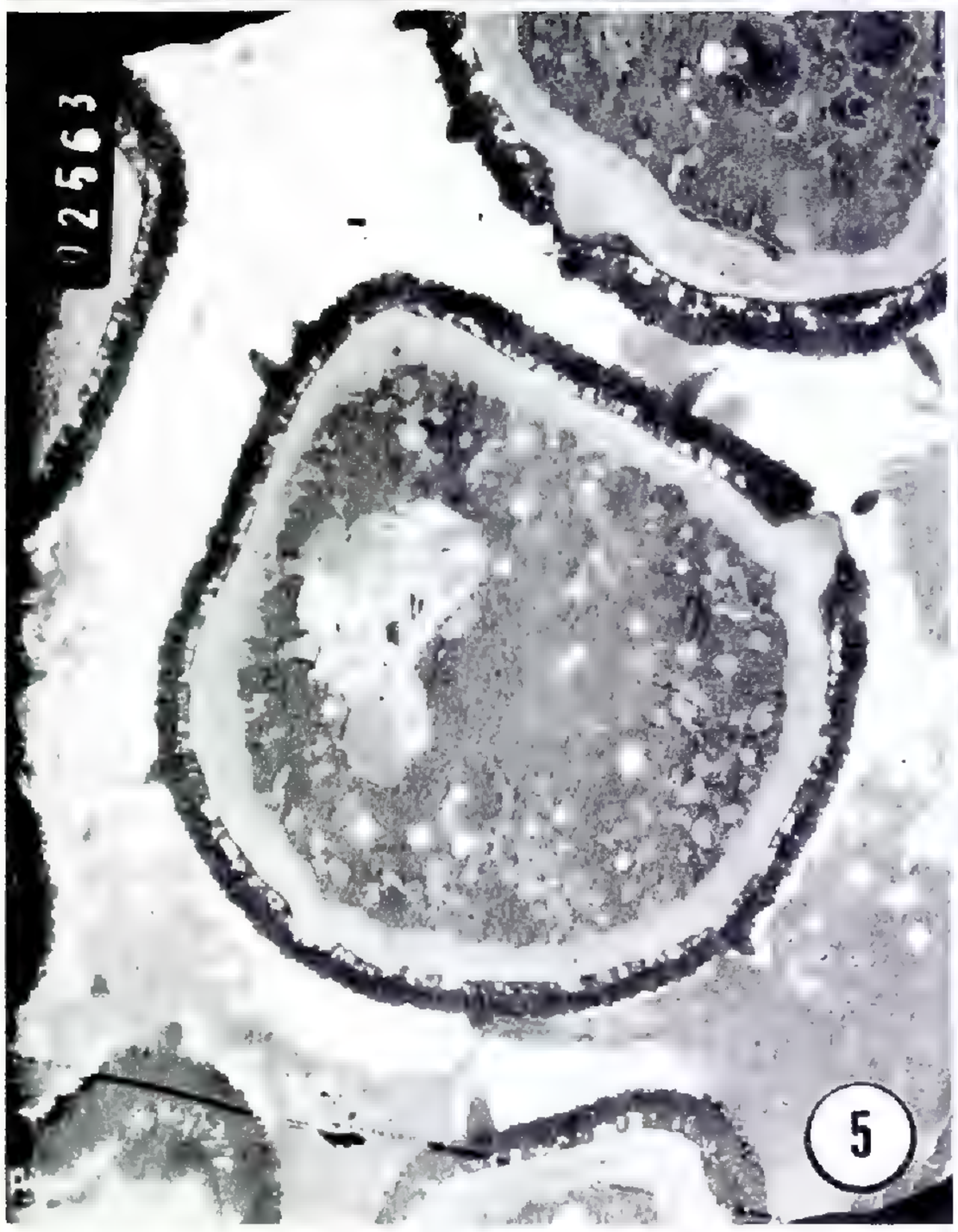
POLLEN

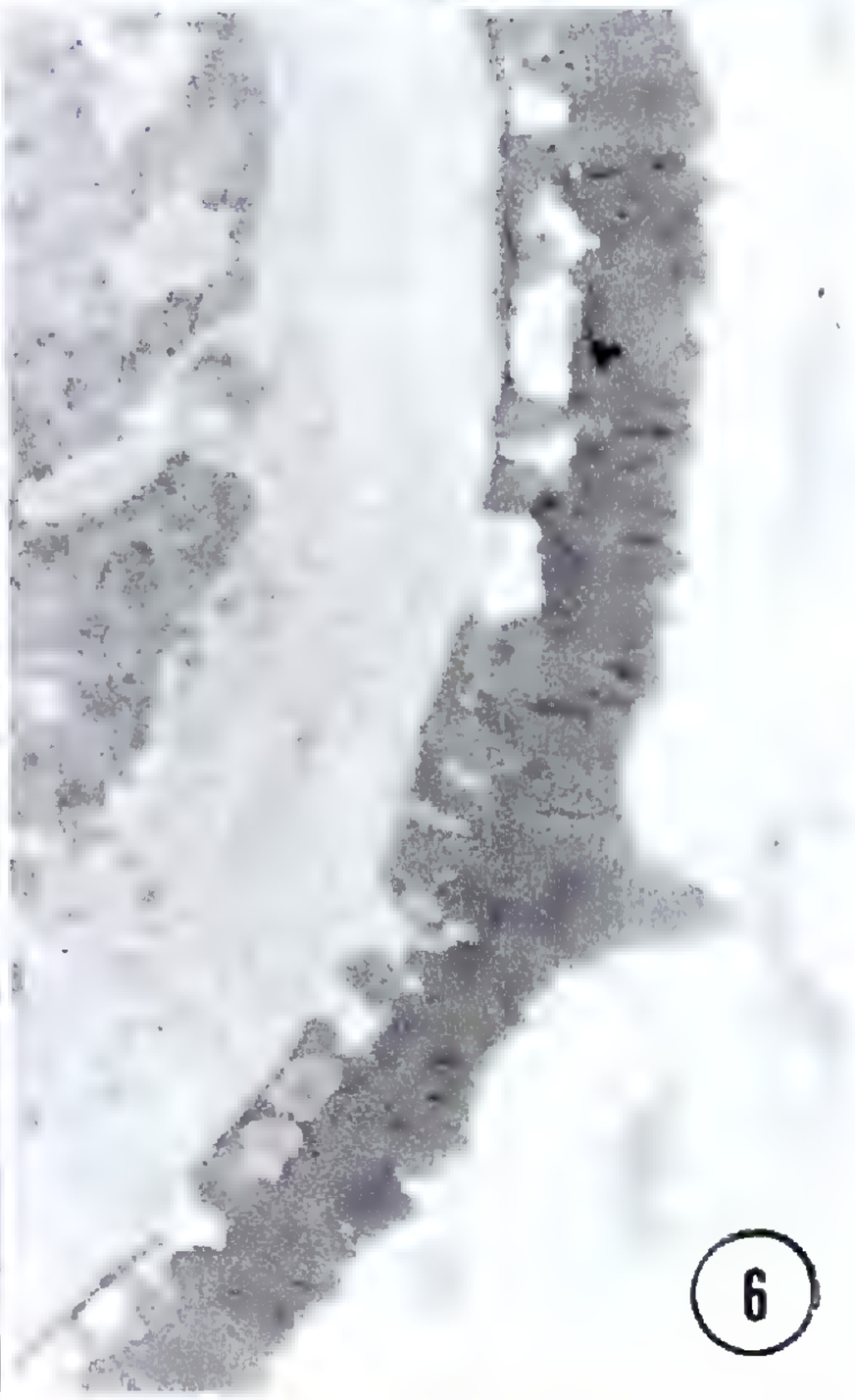
PICRODENDRON (FIGURES 3–9). The pollen of *Picrodendron baccatum* was described by Erdtman (1952) as 5- to 8-colporate, oblate-spheroidal, with an average diameter of 34 μm, spinuliferous, with sexine thicker than nexine, and with ectosexine thicker than endosexine. We have refined this brightfield microscope description based on whole mounts and epoxy sections stained in basic fuchsin: Pollen grains 5- to 8-zonicolporate, radially symmetrical, isopolar, oblate-spheroidal, 26 × 29 μm. Amb circular. Colpi short, L:W ratio 4:1 or less, ora lalongate to circular. NPC: 545, 645, 745, 845. Exine spinose, tectate-perforate. Ectosexine about twice as thick as endosexine. Nexine extremely thin and discontinuous.

Electron microscope (SEM and TEM) observations add substantially to the understanding of *Picrodendron* pollen: Exine sculpturing echinate, the spinules to 3 μm long, well spaced, with clusters of 3 to 5 around colpi, the interspinule area densely verrucate. Ectosexine 0.6–0.8 μm thick, structured from more or less cylindrical rods, with bacula incompletely fused distally, the tectal surface verrucate, traversed to varying degrees by irregular channels, some of which coincident with gaps in endosexine and nexine to form intact passage to surface. Endosexine 0.2–0.4 μm thick, tapering to extinction near aperture, with narrow to broad columnar struts unevenly spaced, fused in massive columns in few areas, absent in other areas so nexine only loosely attached. Nexine extremely thin, 0.06–0.25 μm, serving as footlayer for endosexinous struts, frequently discontinuous in mesocolpial regions, forming pronounced wedge-shaped thickenings of 2 distinct layers near aperture: nexine-1 (footlayer in contact with endosexine), with point of thickening initiated about 1 μm from colpus rim, becoming lamellate at edge of os, extending across aperture in both acetolyzed and unacetolyzed grains; nexine-2, with thickening moderate, initiated about 1 μm from edge of os, appearing to extend across aperture in acetolyzed and unacetolyzed grains to form thin membrane. Intine as thick as or thicker than exine, 1–2 μm, divisible into 2 layers, outer one less electron dense, inner one granular. Intine relatively thin in mesocolpial regions, normally abutting nexine, but extending through gaps to contact sexine directly, expanding into lens-shaped thickening in aperture region and protruding up through os.

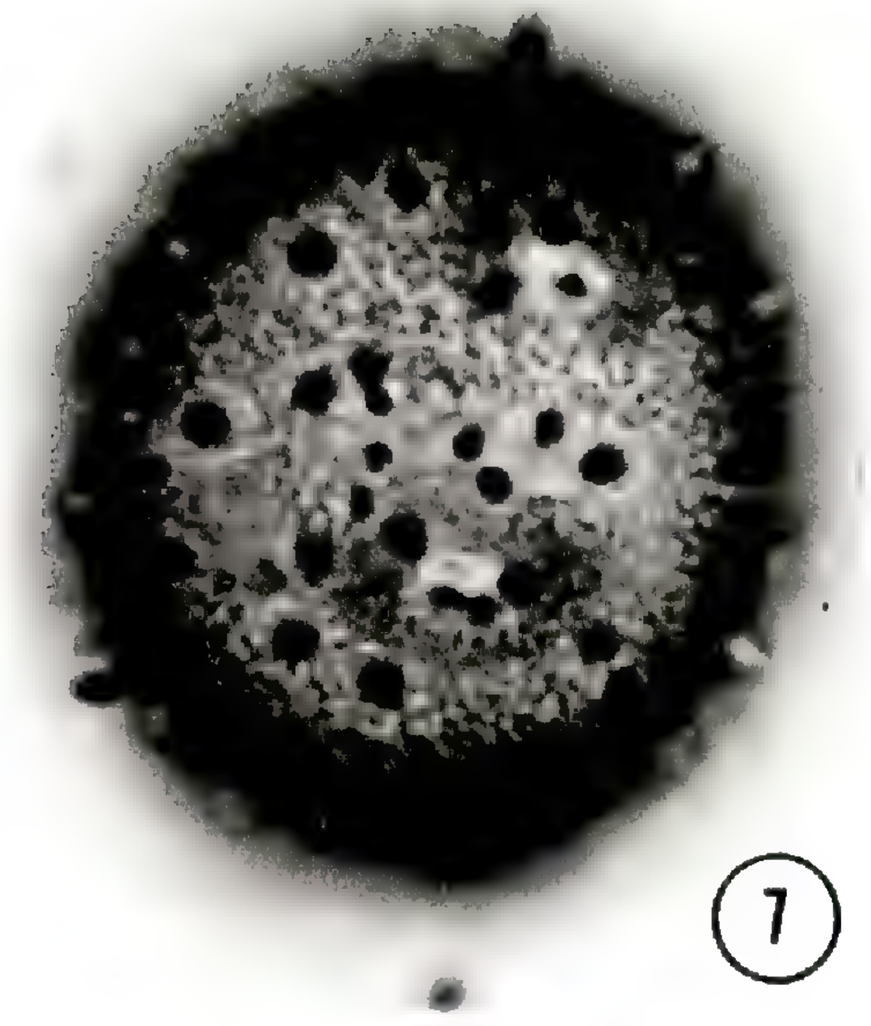
OLDFIELDIOIDEAE (FIGURES 10–20). Erdtman (1952) first surveyed several members of the subfamily, but Köhler's (1965) treatment of the pollen morphology of the biovulate Euphorbiaceae is quite comprehensive and serves in a substantial way to document the brightfield microscope observations. The chief difference between Köhler's description and our study is reflected in the NPC formulae for the group: we interpret the grains as brevicolporate instead of

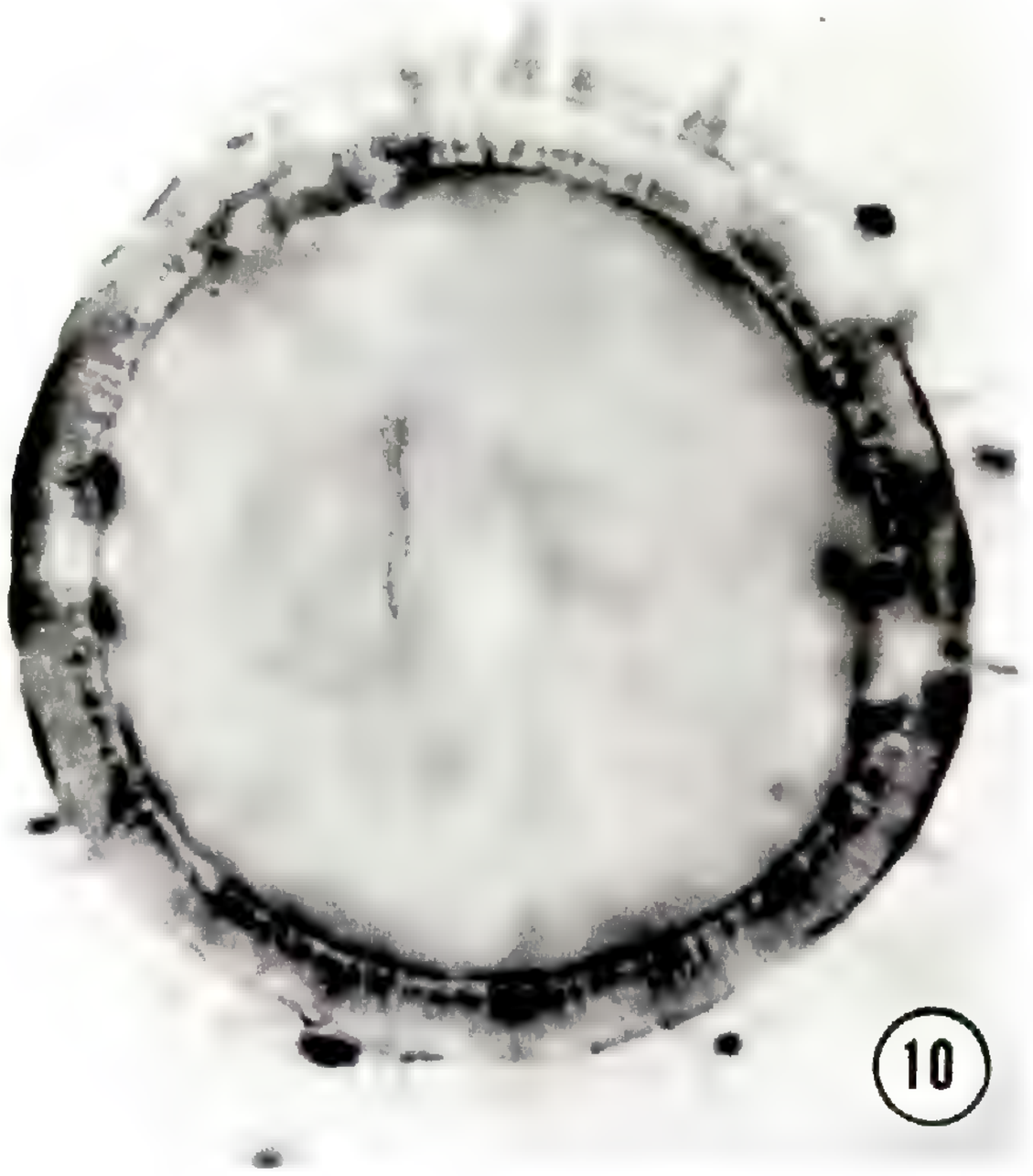






FIGURES 3–6. Pollen of *Picrodendron baccatum.* 3, *Harris 12516,* scanning electron micrograph of acetolyzed grain showing 2 slightly elongate pores, × 1800. 4–6, transmission electron micrographs of *Clemente 6587*: 4, acetolyzed grain, × 4000; 5, glutaraldehyde-OsO_4-fixed grain, × 2200; 6, glutaraldehyde-OsO_4-fixed grain, × 10,000.

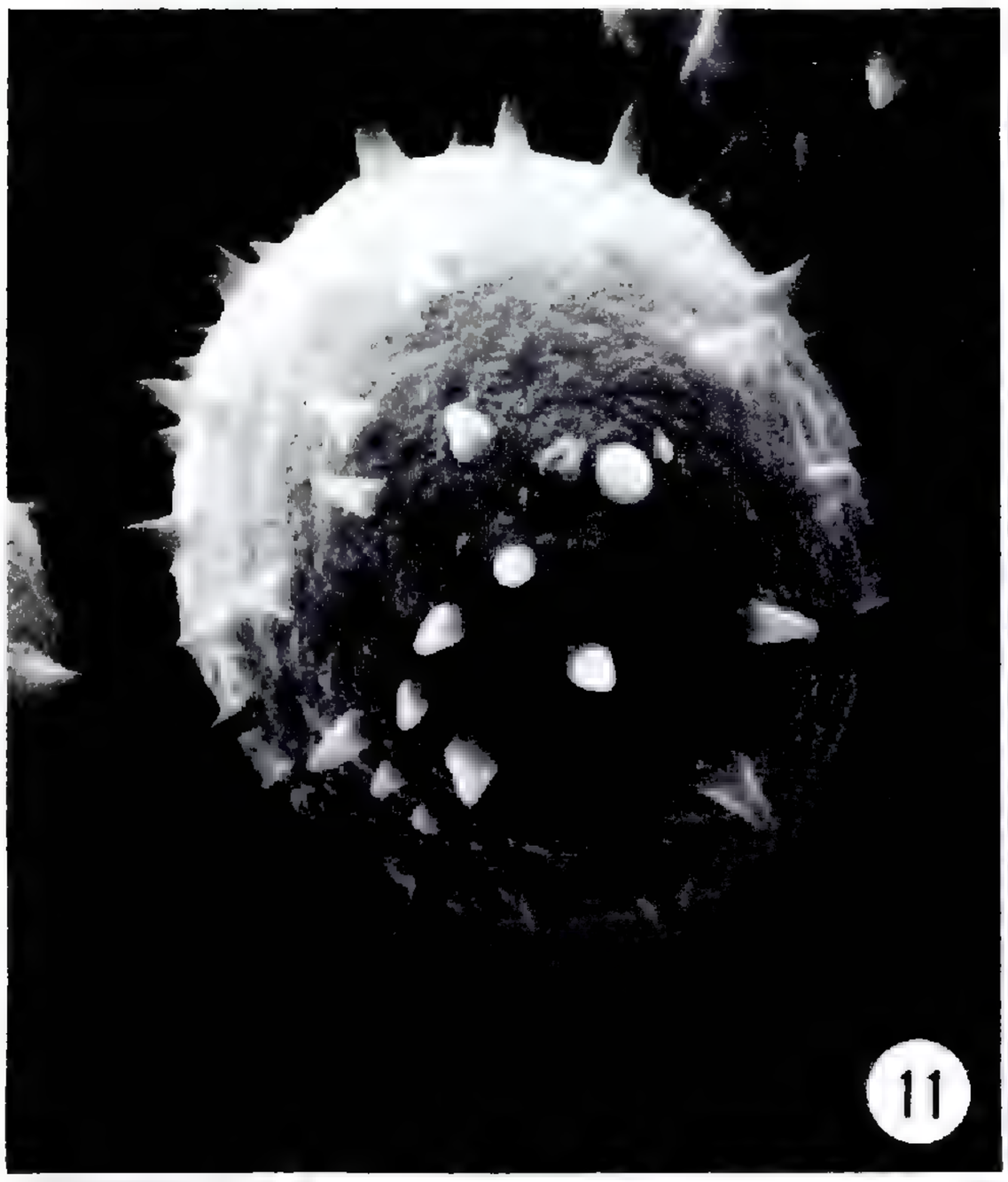


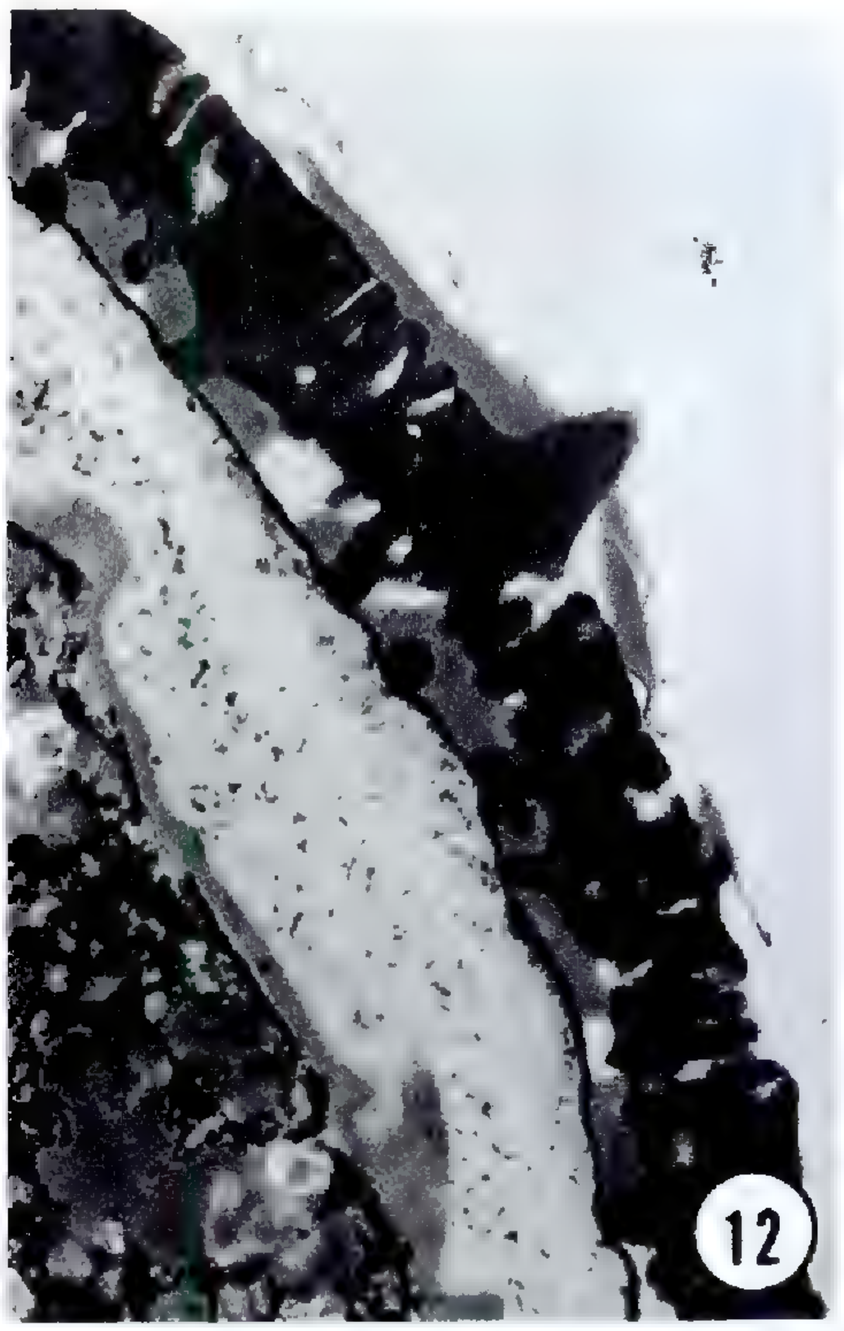


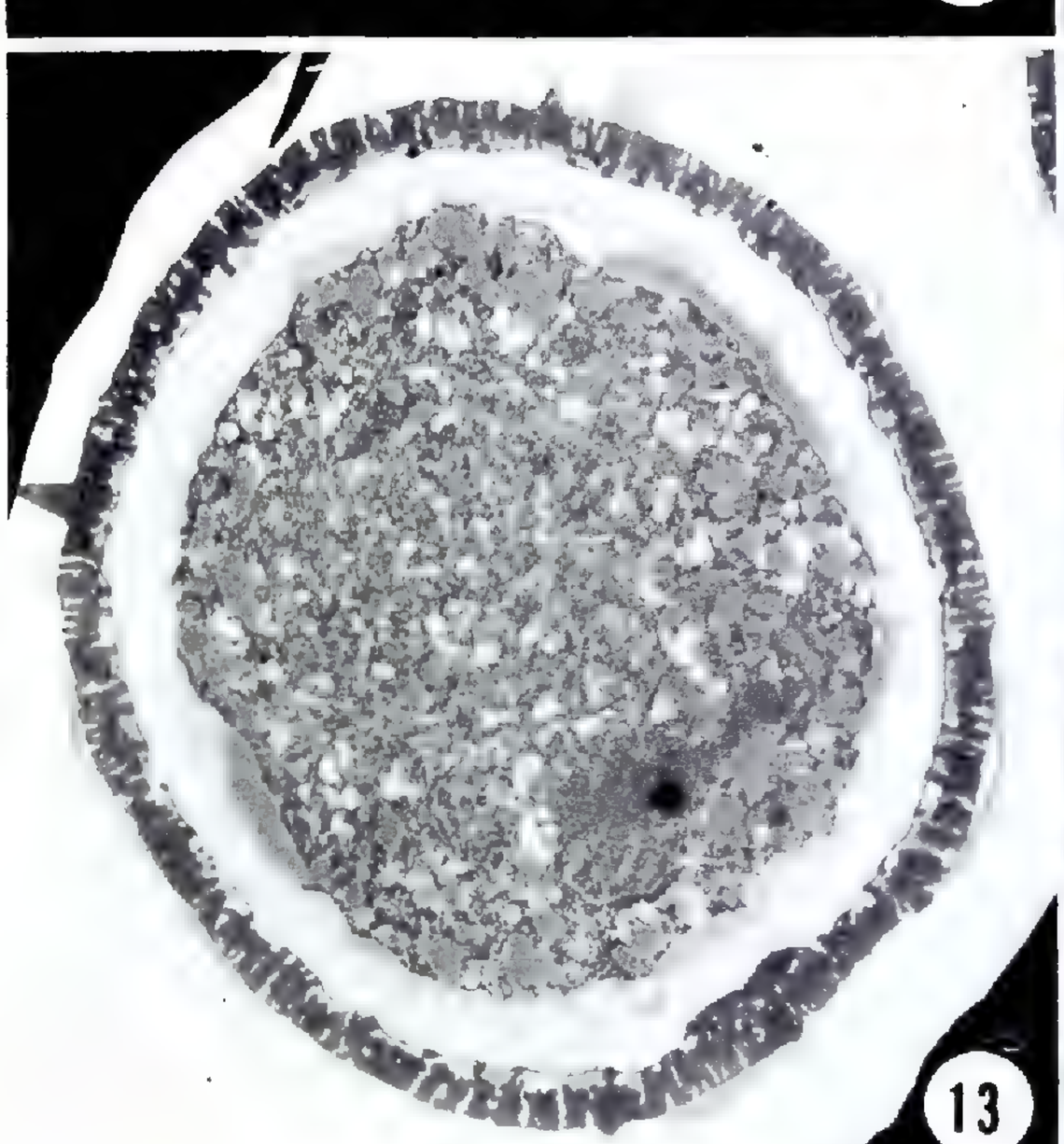
FIGURES 7–10. Brightfield photomicrographs of pollen, × 1480. 7–9, *Picrodendron baccatum* (*Clemente 6587*), single acetolyzed grain (whole-mount): 7, top focus, showing 2 short colpi; 8, optical cross section; 9, lower focus showing outline of 2 ora. 10, *Austrobuxus carunculatus* (*Hürlimann 571*), acetolyzed grain at optical cross section, nexine thickenings prominent at aperture.

simply colpate. The apertures, whether elongate or not, are all distinctly compound, and we see no reason not to consider the nexine opening in each aperture as an os. Köhler refers to the os in his general description of his "*Tetracoccus*-type" of pollen, but he calls it an "oroid" in his "*Longetia*-type."

Based on our generalized brightfield microscope observations of the taxa listed above, oldfieldioid pollen can be described as follows: 4–7 zoniporate

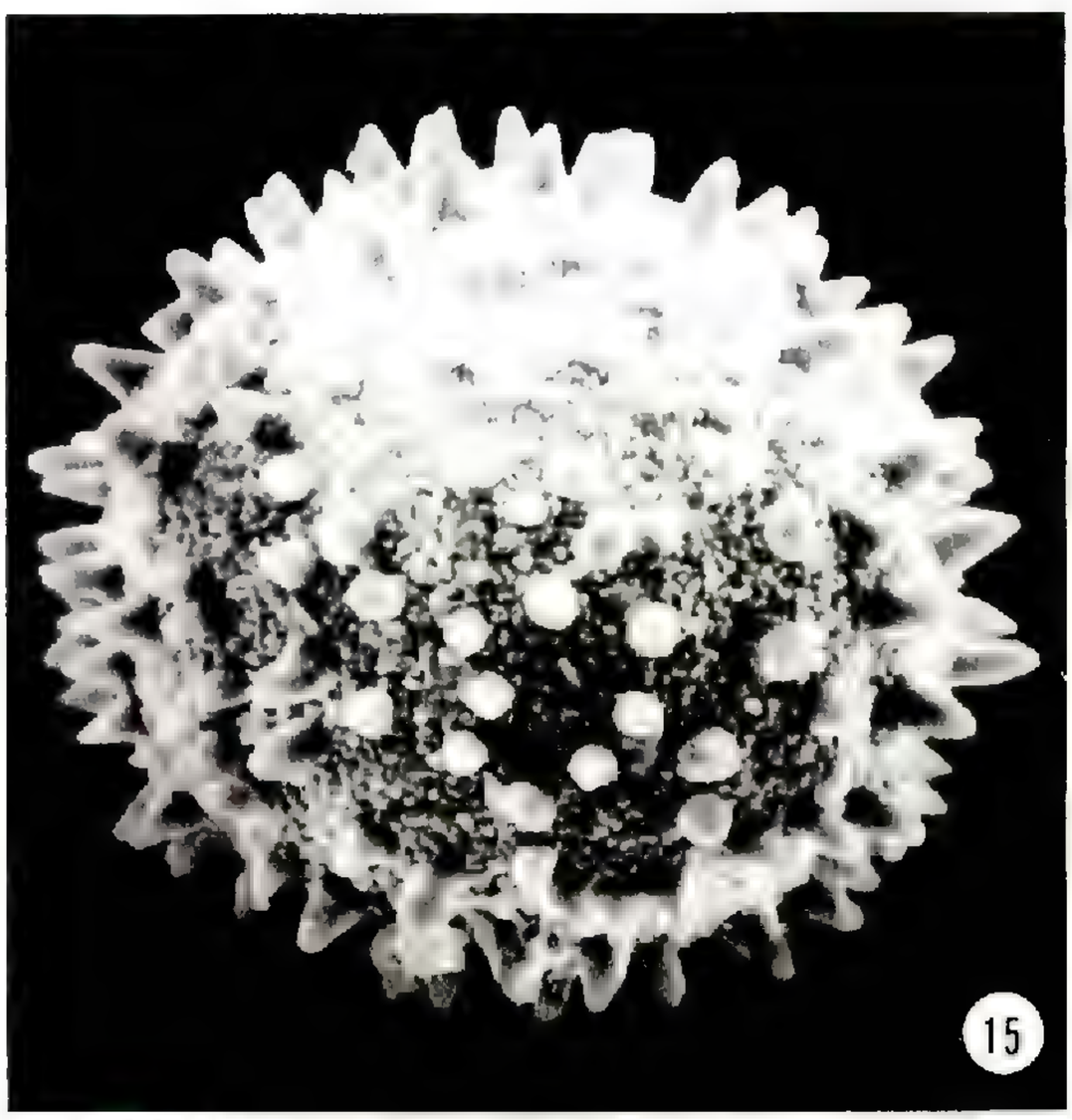


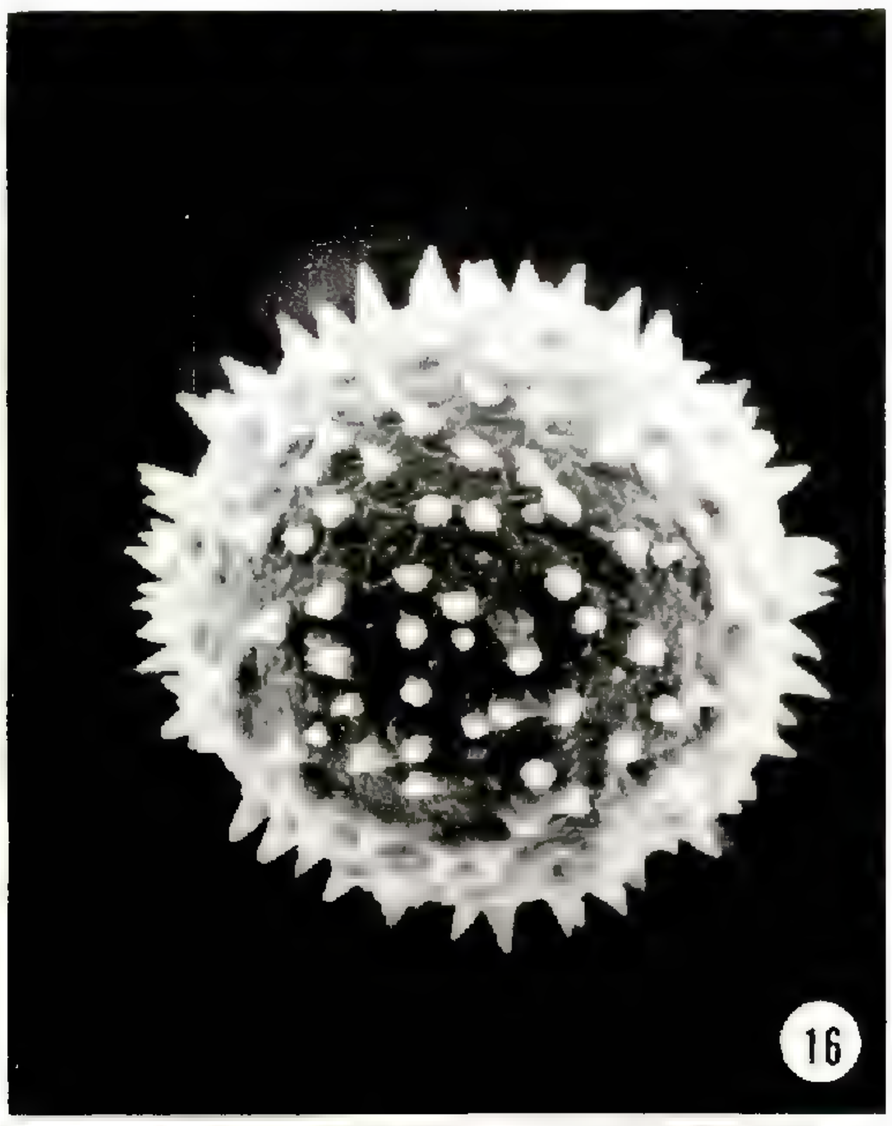


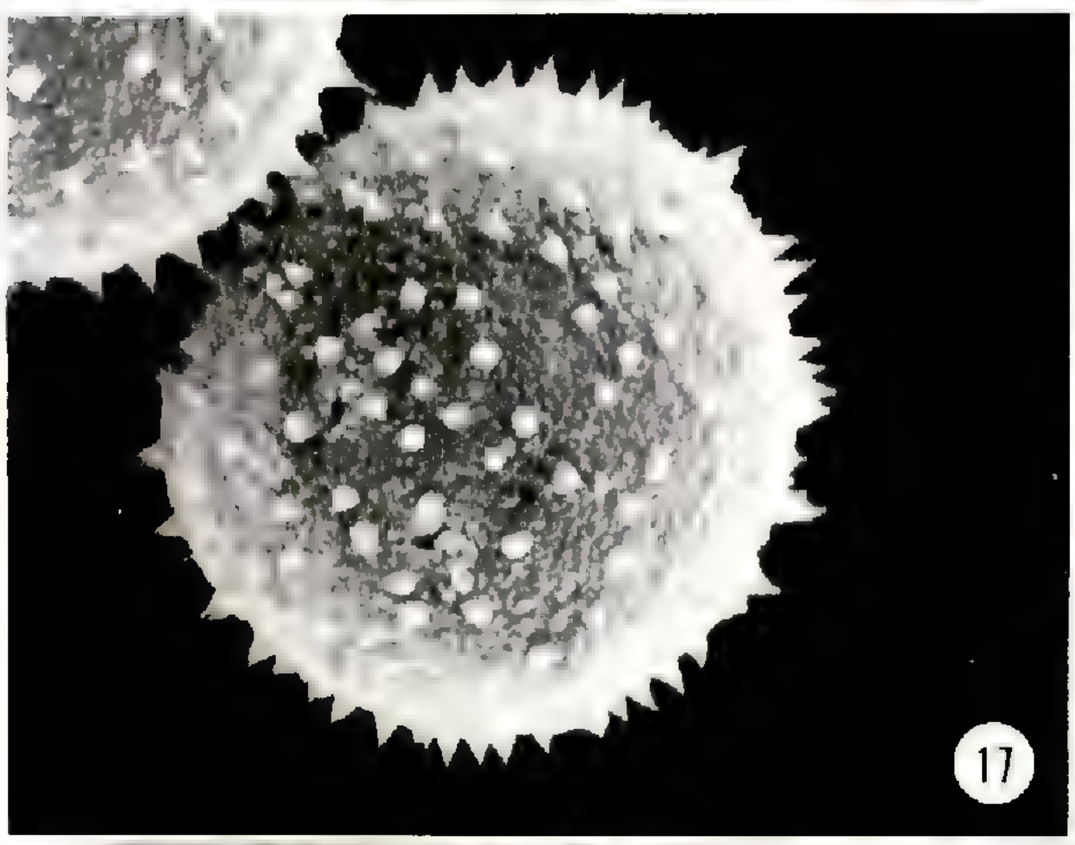


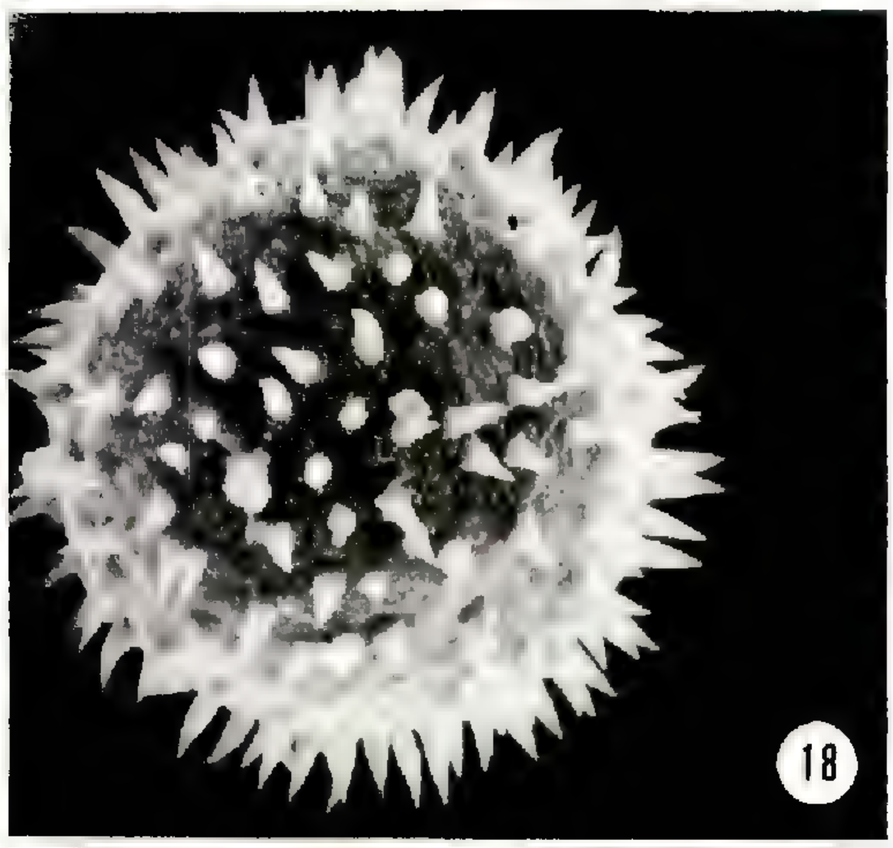
FIGURES 11–14. Pollen of *Austrobuxus carunculatus*. 11, *Hürlimann 571*, scanning electron micrograph of acetolyzed grain, × 1720. 12–14, *Stauffer & Blanchon 5751*, transmission electron micrographs of grains fixed in glutaraldehyde-OsO_4: 12, × 6000; 13, × 1800; 14, × 6000.

to colpororate, radially symmetrical, isopolar or paraisopolar, oblate-spheroidal to suboblate, medium size (25–40 μm). Amb circular. Colpi lolongate, very short and inconspicuous (L:W ratio 3 : 1 or less), both colpi and pores often indistinct. Ora usually larger than colpi, lalongate, round, or lolongate, delim-









FIGURES 15–20. Scanning electron micrographs of acetolyzed pollen grains of species of Euphorbiaceae subfam. Oldfieldioideae: 15, *Tetracoccus dioicus* (*Munz 12614*), × 1360; 16, *Oldfieldia africana* (*Voorhoeve 1963*), × 1360; 17, *Tetracoccus hallii* (*Kearney & Harrison 7530*), × 1360; 18, *Piranhea longepedunculata* (*Blanco 299*), × 1360; 19, *Austrobuxus eugeniifolius* (*Guillaumin & Baumann-Bodenheim 12908*), × 1560; 20, same collection as in FIGURE 19 but different grain, showing detail of aperture, × 4080.

ited and more or less ringed by nexine thickenings formed by several more or less contiguous granules, these thickenings confined to polar ends of colpi in some species, to continuous ring or annulus around entire circumference in others. NPC: 445, 545, 645, 745. Exine tectate-perforate. Sexine much thicker than nexine, with broad-based, solid spines or spinules distributed more or less evenly over verrucate tectum except for clusters around apertures. Endosexine baculate, bacula ramifying distally and fusing to form incomplete tectum. Nexine very thin and occasionally discontinuous, but with prominent thickenings around apertures.

A limited sampling of five genera with SEM and one sample of *Austrobuxus carunculatus* with TEM yields the following ultrastructural description of Oldfieldioideae pollen: Exine sculpturing echinate, the spinules prevalent, becoming spines to 4.1 μm in *Austrobuxus carunculatus*, generally sharp pointed (rounded in some specimens of *Tetracoccus dioicus*), well spaced, the interspinule area sparsely (*Mischodon zeylanicus*) to densely verrucate. Ectosexine 0.9–1.4 μm thick, structured from more or less cylindrical rods, these irregularly fused to form relatively porous, bumpy tectal surface (verrucate) traversed to varying degrees by numerous channels (perforate). Endosexine 0.1–0.4 μm thick, terminating near aperture rim, with narrow to broad columnar struts unevenly spaced so nexine appears loosely attached. Nexine extremely thin, 0.06–0.12 μm, serving as footlayer for endosexinous struts, mostly continuous in interaperture region, forming pronounced wedge-shaped thickening of 2 distinct layers near aperture: nexine-1 (or footlayer in contact with endosexine), with point of thickening initiated ca. 1 μm from edge of os, appearing to extend across aperture in unacetolyzed grains as uniformly thin layer; nexine-2, with thickening initiated ca. 1 μm from edge of inner aperture, apparently terminating abruptly to form os. Intine as thick as or thicker than exine, 1–2 μm, divisible into 2 layers as in *Picrodendron* (inner, electron-dense area much thinner in intercolpial regions than in *Picrodendron*; outer, in contact with nexine, generally thick throughout grain and sprinkled with electron-dense granules and short rods).

DISCUSSION OF RELATIONSHIPS

Relationships at the Familial Level

Picrodendron conforms more closely with the Euphorbiaceae than with any other family to which relationships have been proposed—a conclusion supported by gross morphology, pollen, and chromosome number (discussed below), as well as by vegetative anatomy (Hayden, 1977).

The reduced unisexual flowers of *Picrodendron* fit easily within the enormous range of floral diversity exhibited by the Euphorbiaceae. The strength of this association, however, is in the presence of pendulous anatropous ovules with a ventral raphe and a micropylar obturator (Figure 2, I), characters diagnostic for the Euphorbiaceae. Fawcett and Rendle (1917) first pointed out these facts, but their conclusion of euphorbiaceous relationships for *Picrodendron* received delayed recognition because of their erroneous description of the ovary as

inferior. Although this mistake was soon corrected (Fawcett & Rendle, 1920), the damage had already been done: Pax and Hoffmann (1931) excluded *Picrodendron* from the Euphorbiaceae largely because they repeated Fawcett and Rendle's inaccurate perception of ovary position. This unwarranted exclusion from the family by such prominent authorities discouraged any serious reconsideration of relationships with the Euphorbiaceae for several decades.

The absence of floral discs and of endosperm in mature seeds is unusual for the Euphorbiaceae, but these conditions are not unknown in the family. Also, *Picrodendron* is unusual (but not alone) within the Euphorbiaceae in having a drupaceous fruit instead of the more common schizocarpous capsule. These divergences are few; far more characteristics would have to be reconciled if *Picrodendron* were to be placed in any of the other families to which it has been assigned in the past (see Hayden, 1977, for detailed comparisons with some other families).

Erdtman's (1952) comment on the similarity of *Picrodendron* pollen with that of *Pseudanthus* Sieber ex Sprengel is largely responsible for revitalizing the notion of a relationship with the Euphorbiaceae. Indeed, the obvious similarities in pollen wall sculpturing and architecture between *Picrodendron* and certain Euphorbiaceae argue for a close relationship. On the other hand, *Picrodendron* shares few pollen features with the Juglandaceae (Stone & Broome, 1975) or the Rhoipteleaceae (Stone & Broome, 1971), with which it has been associated (Cronquist, 1968; Hutchinson, 1973), and it is not similar to the Simaroubaceae (Erdtman, 1952). Of particular note are the granular elements in the Juglandaceae ("structure grenue" of Van Campo & Lugardon, 1973) that are fused in varying degrees to form the columellae of the endosexine region. The bacula of *Picrodendron* and *Austrobuxus* Miq. are typical cylindrical rods; they may vary in size but would never be characterized as granular. The perforate ectosexine of *Picrodendron* and *Austrobuxus* is in marked contrast to the homogeneous tectum of the Juglandaceae, which is without pits or pockets except for the ultrafine channels that traverse the wall (Stone *et al.*, 1964). These aspects, as well as the more obvious differences in pollen sculpturing and aperture construction, leave little doubt that *Picrodendron* has more in common with the Euphorbiaceae than it does with the Juglandaceae. Overall, pollen of *Picrodendron* falls easily within Köhler's (1965) "*Tetracoccus*-type" of Euphorbiaceae subfam. Oldfieldioideae.

Relationship with the Oldfieldioideae is also confirmed cytologically. Fritsch (1972) reported a chromosome number of $2n = 48$ for *Picrodendron*. Members of the Euphorbiaceae-Oldfieldioideae are not well known cytologically, but published counts of $n = 24$ for *Mischodon* Thwaites and $2n = 24$ for *Tetracoccus* Engelm. ex Parry (Hans, 1973) suggest that the count for *Picrodendron* is consistent with a base number of 12 for the subfamily. On the other hand, members of the Juglandaceae—with the exception of several tetraploid hickories in *Carya* Nutt. sect. CARYA—are uniformly $n = 16$ (Stone & Broome, 1975). The Simaroubaceae have an assortment of chromosome numbers: reports of $n = 12$ are known for *Brucea* J. F. Miller and *Picrasma* Blume, $n = 13$ for *Castela* Turpin, $2n = 26$ for *Holacantha* A. Gray, $n = 16$ for *Simarouba* Aublet, $2n = 26$ for *Klainedoxa* Pierre, $2n = 28$ for *Irvingia* Hooker f., $2n =$

36 for *Quassia* L., and $n = 31$, $2n = 62$, 86 for *Ailanthus* Desf. (Darlington & Wylie, 1955; Moore, 1973, 1977). Of these simaroubaceous genera, only *Klainedoxa* and *Irvingia* were ever closely associated with *Picrodendron* (Hayden, 1977), but the known chromosome counts do not support such a relationship.

The paucity of fossils in most angiosperm groups tends to confer special significance upon any known fossils. Thus, the discovery of fossilized seeds and fruits of *Rosenkrantzia picrodendroides* B. Koch from the Cretaceous-Tertiary boundary of West Greenland is of interest because of their resemblance to *Picrodendron* (Koch, 1972). The fossil fruits are interpreted as either nuts or drupes and contain one or two seeds encased in a tough, woody pericarp (mesocarp?). The seeds are pendulous from an apical placenta and contain folded cotyledons but no endosperm. Presence of long-petiolate, trifoliolate leaves in associated fossil beds suggests an even greater list of similarities with *Picrodendron.* Although the fossil is unicarpellate and *Picrodendron* is bicarpellate, Koch was not deterred from perceiving a close relationship between these plants; furthermore, this disparity prompted an elaborate hypothetical derivation of both plants, consistent with Small's (1917) placement of the Picrodendraceae between the Juglandaceae and the Fagaceae.

Koch's thesis is difficult to evaluate, partly because of its complexity but mainly because of its awkward use of several morphological terms. For example, the pedicel is consistently referred to as a petiole; possible dehiscence mechanisms are discussed at some length, yet the fruit of *Rosenkrantzia* is described as a nut or drupe; the unicarpellate fruit is interpreted as having four dehiscence valves; and a protuberance on the fossil seed is described as a style base. Koch's hypothetical derivation involves the fusion of paired, reflexed, unicarpellate flowers such that basal placentation (as in the Juglandaceae) gave rise to the apical placentation of *Picrodendron.* At the gross morphological level we know of no evidence that convincingly supports the special criteria of Koch's hypothesis. Finally, as a consequence of his concepts of placentation in *Picrodendron,* Koch ultimately concluded that the resemblances of fruits of *Rosenkrantzia* and *Picrodendron* are merely superficial; we feel compelled to observe that such a conclusion seriously erodes the original basis for Koch's own hypothesis.

Consequently, the existence of *Rosenkrantzia* does not strengthen the association of *Picrodendron* with the Juglandaceae, and we are disinclined to perceive any relationship between *Rosenkrantzia* and *Picrodendron,* although a reevaluation of this conclusion may be necessary if the four obscure valves of *Rosenkrantzia* prove to be evidence for a multicarpellate condition. Our proposed relationship with the Euphorbiaceae requires no elaborate derivation and is thus simpler than Koch's hypothesis.

Relationships within Euphorbiaceae

The presence of two ovules per carpel and spiny pollen grains indicates that the proper placement of *Picrodendron* is within subfamily Oldfieldioideae (Webster, 1967). In a conspectus of suprageneric taxa of the Euphorbiaceae, Webster (1975) assigned *Picrodendron* to a monogeneric tribe within this subfamily.

In searching for the nearest relative of *Picrodendron* within the Oldfieldioideae, we are impressed with certain similarities to the tribe Hyaenancheae (Baillon ex Mueller-Arg.) Hutchinson, especially to members of subtribe Paivaeusinae Pax & Hoffm. According to Webster's (1975) classification, the Paivaeusinae includes *Aristogeitonia* Prain and *Oldfieldia* Bentham, from Africa; *Celaenodendron* Standley, from Mexico; and *Piranhea* Baillon, from northern South America. Airy Shaw (1966, 1973) has associated these genera with *Picrodendron.* Not only do they have compound leaves similar to those of *Picrodendron,* but they are also closest anatomically (Hayden, 1977, 1980) and palynologically. Webster and Lynch (unpubl.), in a more comprehensive survey of Oldfieldioideae pollen than is presented here, reached the same conclusion concerning palynological similarity of *Picrodendron* and the Paivaeusinae. On the basis of a combination of several morphological characters, especially the alternate, stipulate, strictly trifoliolate leaves, dioecy, and elongate styles, *Picrodendron* appears closer to the South American genus *Piranhea* than it does to the African *Aristogeitonia* or *Oldfieldia.* Some features of leaf anatomy of *Picrodendron* likewise compare most closely with *Piranhea,* but certain wood features are better matched by *Oldfieldia* (Hayden, 1977, 1980). In view of the obviously reticulate nature of relationships in the Oldfieldioideae, this does not appear to be a very serious discrepancy.

Despite the above-mentioned similarities with the Paivaeusinae, *Picrodendron* differs from all of the genera of Hyaenancheae in having a distinctive cluster of reproductive characters: staminate flowers with reduced calyx, borne in aments; floral disc absent in both sexes; styles elongate and basally connate; and drupaceous fruits with large, ecarunculate seeds containing plicate cotyledons. On morphological grounds, therefore, *Picrodendron* appears sufficiently divergent within subfam. Oldfieldioideae to be recognized on its own. This reasoning led Webster (1975) to establish the tribe Picrodendreae (Small) Webster. However, when the Oldfieldioideae as a whole are better known, the strength of evidence from anatomy and palynology may prove sufficient to classify *Picrodendron* as an advanced subtribe adjacent to the Paivaeusinae within tribe Hyaenancheae.

It may be speculated that the distinctive reproductive characters of *Picrodendron* reflect an adaptive shift from insect to wind pollination. However, the lack of reduction of spines in the pollen is rather curious, since it is contrary to the trend evident in other taxa of anemophilous Euphorbiaceae (e.g., Hyaenancheae subtribe Dissiliariinae Pax & Hoffm., or many genera of tribe Acalypheae Dumort.). Possibly there is some sort of balance between wind and insect pollination in *Picrodendron,* a hypothesis that needs testing by field observation.

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APPENDIX. **Picrodendron specimens examined.**

Bahama Islands. GREAT ABACO: Old Ken's Pt., *Brace 2029* (F). ANDROS: Coconut Pt., Conch Sound, *Northrop & Northrop 453* (A, F, GH); Deep Creek, *Brace 5198* (F, NY); coppice near Fresh Creek, *Small & Carter 8833* (F, G, P, US); Morgan's Bluff, low thickets inland from rocky sea cliff, *Proctor 30788* (IJ); Driggs Hill, *Popenoe s.n.*, May 1965 (FTG). CAT: whiteland scrub, the Bight, *Britton & Millspaugh 5884* (F, NY); Industrious Hill, side of cliff near caves, *Byrne 323* (A); Port Howe plantation house, *Byrne 364* (A); ledges in open coppice N of Stevenson, *Correll 46153* (F, FTG). ELEUTHERA: rocky plains, vic. of Miller's, *Britton & Millspaugh 5593* (F, NY). EXUMA CHAIN, GREAT GUANA CAY: *Britton & Millspaugh 2895* (F, GH). LONG: Clarence Town, *Britton & Millspaugh 6258* (F, US). NEW PROVIDENCE: *Brace 477* (NY); Paradise Is., center of island, remnant of coppice, *Gillis 11991* (A, IJ).

Cayman Islands. GRAND CAYMAN: logwood woodland on limestone pavement, 0.5 mi N of Joe Conger, *Brunt 1783* (BM, IJ); along track between Old Isaacs and Wintersland, *Proctor 15248* (BM, GH, IJ); 1.5 mi WNW-NW of Brechers, S of Joe Conger, *Proctor 27976* (IJ); E end of island on cliff, *Kings 131* (BM). LITTLE CAYMAN: Snipe Point, dry, rocky woodland, *Proctor 28038* (BM, IJ); S side of Blossom Pt., *Kings 77* (BM, NY). CAYMAN BRAC: W end, edge of dense woodland, *Proctor 29125* (IJ).

Swan Islands. GREAT SWAN: lat. 17°25′N, long. 83°56′W, *Proctor 32534* (BM, IJ).

Cuba. CAMAGÜEY: Silla de Cayo, Cayo Romano, *Shafer 2505* (BM, F, GH, NY, P, US); Santa Lucia, *Shafer 965* (NY); Cayo Sabinal, *Shafer 1107* (BM, F, NY, US). HABANA: Marianao Beach, coastal thickets, *León s.n.*, Feb. 1921 (GH); Pr. Jaimenito, *Ekman 1207* (G, S, US). ORIENTE: Sardinero, coastal thickets, *Clemente 6587* (GH, US); Manigua Costera, Plaza de Puerto Padre, *Lopez 26* (US); Guantanamo Bay, U.S. Naval Station, *Britton 2259* (NY); Santiago de Cuba, Sardinero, wayside coastal thickets, *Clemente 6604* (GH); Santiago de Cuba, Juragria Beach, coastal cliff, *Clemente 7436* (GH, US); Santiago de Cuba, Siboney, in calcareous soil, *Ekman 8710* (F, US); Santiago de Cuba, near El Nacro along seacoast, *Ekman 9195* (F, G, US); Banes, Puerto Rico, coastal forest, *Ekman 6625* (F, G, US); San Germán, along railroad in forest, *Ekman 6344* (G); Cabo Cruz, coastal thickets, *León 16351* (GH, IJ, US); Punta Piedra, Nipe Bay, *Britton et al. 12460* (F, GH, NY, US). PINAR DEL RÍO: Bahía Honda, Finca Toscano, coastal thickets, *Alain 1803* (GH, IJ, US). LAS VILLAS: Cienfuegos, Caunao R., Iguana Point, *Jack 5126* (A, P, US); Caunao R. to Cienfuegos Bay, *Jack 7516* (F, US); Cienfuegos Bay, Punta Sabanilla, coastal thicket, *Britton et al. 4584* (NY); Punta Diablo, Cienfuegos Bay, *Britton & Wilson 5672* (F); Cienfuegos, Faro Villa Nueva, hills and cliffs, Castillo de Jagua, *Combs 646* (GH); Camino de la Costa, E of Castillo de Jagua, *Howard et al. 249* (A, NY); Soledad, Gavilán, *Jack 5824* (A, P, US); Gavilán, *Rehder 1102* (A, P); along Arimao R., *Bangham s.n.*, 22 July 1929 (IJ). WITHOUT DEFINITE LOCALITY: *Sagra s.n.* (P, Herb. Richard).

Dominican Republic. PROV. AZUA: Monte Río, *Lavastrè 1750* (NY); NE of Azua, *Rose et al. 4042* (NY, US). PROV. BARAHONA: near Barahona, *Fuertes 1535* (BM, F, GH, NY, P, US); Barahona, *Jiménez s.n.* (NY); Beata Is., edge of lagoon on E side, *Howard 12430* (A, BM, US); Beata Is., without further locality, *Ostenfeld 297* (C). PROV. LA VEGA: La Vega City, windbreak, La Escuela de Agricultura, *Padre Cicero et al. 7020* (A, IJ), *Jiménez 7125* (A, F, IJ); Bayacanes, near La Vega City, serpentine hills, 300–350 m, *Liogier 11927* (F, IJ, NY). PROV. MONTE CRISTI: El Tamarindo, Hatillo Palma, *Marcano 5202* (NY, Herb. Jiménez). PROV. PEDERNALES: SE of Cabo Rojo near beach in dogtooth limestone, *Liogier 13910* (NY); Cabo Rojo in thickets, sea level, *Liogier 16872* (NY); Cabo Rojo, *Marcano 4528* (Herb. Jiménez). PROV. EL SEIBO: E of Jovero, between Punta Jíaco and Punta Rey, *Abbott 2872* (US).

Haiti. ÎLE DE LA GONÂVE: Mahautière, edge of mangrove, *Ekman 8685* (C, GH); La Mahautière, *Eyerdam 84* (A, F, GH, US); Dubedon, 200 m, *Buch 1009* (IJ). DÉP. DE L'OUEST: Cabaret, Baie des Moustiques, *Leonard & Leonard 12004* (A, US).

Jamaica. CLARENDON PARISH: Jackson Bay, dry, rocky woodland near sea, *Proctor 29171* (IJ, NY); Jackson Bay, 0.7 mi by road inland, border of salina, *Proctor 32643* (F, IJ); Portland Ridge, limestone near seacoast, *Van der Porten s.n.*, 11 July 1950 (IJ); Portland Ridge, coastal hammock, *West & Arnold 148* (GH). ST. ANDREW PARISH: above Ferry, *Grabham s.n.*, 11 Jan. 1896 (NY); Ferry Peninsula, 100 ft elev., *Campbell 6182* (BM, F); limestone hillside near Ferry, *Harris 12516* (BM, GH, NY, PH, US). ST. CATHERINE PARISH: W base of Port Henderson Hill, scrub woodland, *Proctor 22129* (GH, IJ); Port Henderson Hill, *Webster & Wilson 4929* (A, IJ, US); summit of Port Henderson Hill, ca. 700 ft, thickets, *Proctor 32808* (IJ); Port Henderson Hill, path to Rodney's Lookout, *Adams 12801* (BM); Bracton & Rodney's Lookout, *Gibbs s.n.* (Herb. C. D. Adams); near Ft. Clarence, E side of Great Salt Pond, *Lewis s.n.*, 1 March 1951 (IJ); Old House Point, on rocky limestone, *Du Quesnay 555* (IJ); Portland Ridge near coast, *Howard 12001* (A, IJ, US); Ferry River, Spanish Town Road, *Harris 9046* (F, NY, US); Coleman's Bay, *Tullock 359* (IJ); Great Goat Is., rocky woodland, *Proctor 17437* (A, F, IJ, US); Great Goat Is., *Harris 9313* (A, BM, C, NY), *Harris 12519* (BM, GH, NY, PH, US); Little Goat Is., Old Harbor Bay, near mangrove swamp, *Britton & Hollick 1851* (NY). WITHOUT LOCALITY: *Macfadyen s.n.* (P).

Cultivated. TOBAGO: cultivated at Botanic Station, *Broadway s.n.*, 8 Nov. 1932 (BM). TRINIDAD: Royal Botanic Garden, Port-of-Spain, *Fairchild 2046* (AAH), *Nevling 316* (AAH), *Broadway 7321* (A, AAH, F, NY). U. S. A., FLORIDA, MIAMI: U.S.D.A. Plant Introduction Station, P.I. 98559, M5850, introduced from Trinidad Botanic Garden, *Gillis 7846* (AAH, FTG, IJ), *Fennell 948* (AAH); estate of Mrs. Alvin R. Jennings, *Rehder s.n.*, 30 April 1920 (AAH), *Gillis 9330* (AAH, FTG), *Popenoe 20* (FTG); Fairchild Tropical Garden, introduced from Driggs Hill, South Andros, Bahama Islands, *Gillis 10924, 10975, 11031* (AAH, FTG, IJ).

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THE FIRST SPECIES OF STAURANTHERA (GESNERIACEAE) FROM NEW GUINEA, WITH GENERAL NOTES ON THE GENUS

B. L. BURTT

ALTHOUGH *Stauranthera* Bentham is listed in Willis (1973) as a genus of ten species, on closer study that number proves to have been a little generous. To date, twelve names have been published. *Stauranthera chiritiflora* Oliver has become the type species of *Whytockia* W. W. Sm. (Smith, 1919), and *S. tsiangiana* Hand.-Mazz. also belongs to *Whytockia* (Weber, 1982). Merrill (1923) reduced both *S. ecalcarata* R. Br. and *S. philippinensis* Elmer to synonymy under *S. caerulea* (Blume) Merr., but for the present I am inclined not to include *S. philippinensis* there. *Stauranthera brandisii* C. B. Clarke, described almost simultaneously as *Rhynchotechum brandisii* C. B. Clarke, is of uncertain identity but is not a *Stauranthera* (see Burtt, 1962, p. 37, to which it can now be added that on the isotype at Calcutta, infructescence and leaves are joined, so there is no doubt that they belong together). Finally, I now reduce *S. johannis-winkleri* Kränzlin to a synonym of *S. argyrescens* Hallier f.

This leaves seven species, ranging from northeastern India and Bangladesh to Celebes (Sulawesi): *Stauranthera umbrosa* (Griff.) C. B. Clarke, from NE India, Burma, S China, and the Malay Peninsula; *S. grandiflora* Bentham, from NE India, Bangladesh, Burma, Thailand, the Malay Peninsula, and Sumatra; *S. caerulea* (Blume) Merr., from Sumatra, Java, and (?) Celebes; *S. ionantha* Hallier f. and *S. parvifolia* S. Moore, both endemic to Sumatra; *S. argyrescens* Hallier f., from Borneo; and *S. philippinensis* Elmer, from the Philippines. Some of these records (partly culled from the literature) require verification. I have not seen *S. ionantha* or *S. parvifolia*. The distinction between *S. umbrosa* and *S. caerulea* is not always clear.

The discovery of a distinct species in New Guinea greatly extends the generic range of *Stauranthera*. When a western Malesian genus is discovered in New Guinea, it is natural to seek possible lines of contact as indicated by the affinities of the species. Unfortunately, *S. novoguineensis* does not provide particularly strong clues, especially while the *S. caerulea–S. philippinensis* problem awaits clarification. There seem to be two affinities, as indicated in the diagnosis. One, with the eastern Bornean *S. argyrescens* Hallier f., rests on just a single character that is uniquely shared by these two species: the presence of filiform sclereids (Hallier's "Faserzellen") in the mesophyll. These may be simple or slightly branched toward the tips. They are not known in other species, and since their presence can be detected in the dried leaf by the characteristic ripples on the surface (easily visible with a × 10 hand lens), it seems fairly certain that they

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do not occur. In general facies, especially in leaf shape, *S. novoguineensis* is closer to *S. philippinensis*—a species that lacks sclereids and seems to have slightly different flowers but nevertheless appears to provide the closest affinity for the new species.

An additional floristic link between New Guinea and the Philippines is always of interest and merits comparison with other examples within the family. In *Agalmyla* Blume (incl. *Dichrotrichum* Reinw.) the link is evidenced by the fact that most of the species with long-pedunculate inflorescences are found in New Guinea, the Moluccas, and the Philippines. *Epithema benthamii* C. B. Clarke, described from the Philippines, occurs also on the New Guinea mainland. *Cyrtandra tarsodes* B. L. Burtt, of New Guinea, is most closely related to *C. auriculata* C. B. Clarke, from the Philippines (Burtt, 1971). These two species are rather isolated in the genus as a whole, but in general the much-branched, shrubby New Guinea species of *Cyrtandra* are more closely related to the many species of similar habit in the Philippines than they are to the larger-leaved, single-stemmed species that predominate in Borneo.

In a collection of essays on Wallace's line (Whitmore, 1980), the composition of the eastern Malesian flora and fauna is reexamined in relation to the recent findings on plate tectonics. It is suggested that Australia–New Guinea drifted northward and made contact with the Laurasian outliers of Celebes about 15 million years ago. Celebes may have a central suture, making it half Asiatic and half Australasian. At about the same time, New Guinea collided with a "tertiary island" to the north, eventually resulting in the upthrusting of the central mountain spine; New Guinea is thus also of mixed "parentage."

In the botanical essays in this volume, attention is focused on Wallace's line and on the east-west interchange through the unstable archipelagic area between Celebes and New Guinea termed "Wallacea" by a number of biogeographers; there is no further mention of the "tertiary island" or "tertiary arc" (Raven, 1979) with which New Guinea is said to have collided. If it carried a Philippine-type flora, it could well have been responsible for the New Guinea–Philippine links that Corner (e.g., 1967, p. 45) ascribed on phytogeographic grounds to an old Melanesian foreland.

Stauranthera is a very distinctive genus marked by its strongly plicate calyx and by the cruciform arrangement of its four anthers. It is always strongly anisophyllous, with the small leaf reduced to a lateral auricle. The structure of its shoot and inflorescence has recently been elucidated by A. Weber (1977); he suggests a fairly close affinity to *Loxonia* Jack, with which I certainly agree. *Stauranthera grandiflora* Bentham, the type species of the genus, has a strongly spurred corolla—a feature included in the original generic description but not present in any other species and clearly not of generic significance.

Herbarium material of *Stauranthera* is often inadequate: corollas fall quickly, and the somewhat succulent plants require more careful drying than they sometimes receive. Although a wider range of good specimens is essential before the genus can be satisfactorily revised, the records of two species, *S. argyrescens* and *S. grandiflora,* are extended here.

Stauranthera argyrescens Hallier f. Ann. Jard. Bot. Buitenzorg **13:** 286. 1896. TYPE: Kalimantan, Amai Ambit, ca. 600 m alt., cult. in Horto Bogoriensi, *Hallier B3453* (BO, n.v.).

S. johannis-winkleri Kränzlin, Mitt. Inst. Allg. Bot. Hamburg **7:** 92. 1927. TYPE: West Borneo [Kalimantan], Bukit Mulu, Urwald, ca. 700 m alt., 1 December 1924, *Winkler 453* (HBG, photo E).

SPECIMENS EXAMINED. **Indonesia.** BORNEO. Kalimantan Timur: Central Kutei, Belajan R., G. Kelepoh, near Tabang, forest, sandy yellow loam, in rivulet, 50 m alt., *Kostermans 10429* (L); around Jellini, along S Belajan, NW of Tabang, tropical rain forest, 100–150 m alt., *Murata et al. B1126* (L); Gunung Kongkat–G. Kongbotak, 1°10′N, 116°20′E, lowland rain forest, 150–200 m alt., *Kata & Wiriadinata B5156* (L); W Kutei, G. Kelepoh, near Tabang on Belajan R., yellow loam, low alt., *Kostermans 10596A* (L); E Kutei, S Menubar region, ridge, loam soil with limestone, 30 m alt., *Kostermans 5228* (L).

I have not seen the type of *Stauranthera argyrescens,* but I have little doubt that all the material cited above belongs to this species. Hallier described a plant that flowered in the Botanic Garden after having been transported from Borneo. His illustration suggests a stunted plant that had not fully recovered from the move. The other specimens all have a distinctly pedunculate inflorescence and obvious internodes. Hallier derived his specific epithet from the silvery patches on the leaves—a character not noted by other collectors, but one that is not constant in other rain-forest herbs (cf. Burtt, 1976). This species has distinctive filiform leaf-sclereids that were noted by Hallier and are present in all the material cited, including the type of *S. johannis-winkleri.* They are not known in any other species except *S. novoguineensis* (described below).

Stauranthera grandiflora Bentham, Scroph. Ind. 57. 1835—sphalmate "grandifolia"; C. B. Clarke *in* A. & C. DC. Monogr. Phanerog. **5:** 190. 1883, and *in* Hooker f. Fl. Brit. India **4:** 371. 1884. TYPE: Penang, *Wallich 6395* (K).

Glossanthus? grandiflorus Bentham *in* Wallich, Num. List, 6395. 1832, nomen nudum.

GENERAL DISTRIBUTION. Thailand, Burma, Bangladesh, Malay Peninsula, Sumatra.

NEW RECORDS. **India.** GREAT NICOBAR IS.: Laful, rocky streambed inside dense forest, 10 m alt., *Hore 8777* (E, PBL). **Malay Peninsula.** SELANGOR: Ulu Gombak, descent to river at mile 22, ca. 427 m alt., *Burtt & Woods B1610* (E).

The species has not previously been recorded from the Nicobar Islands. The record from Ulu Gombak is new merely from a local point of view: the species is not in Henderson's list of Kuala Lumpur plants (Henderson, 1928).

This species is often referred to as *Stauranthera grandifolia,* as it was originally printed. However, C. B. Clarke reported that Bentham himself admitted that this was a printing error, and the citation of the earlier *Glossanthus? grandiflorus* at the time of publication confirms this. The species should therefore be known as *S. grandiflora.*

Stauranthera novoguineensis B. L. Burtt, sp. nov.

Stauranthera philippinensi Elmer affinis, sed ovario ellipsoideo glabro (nec sphaerico pubescente), stylo longiore, stigmate bilamellato (nec capitato), foliis sclereidis filiformibus praeditis distinguenda. S. argyrescens Hallier f., sclereidis foliorum S. novoguineensi congruit sed habitu humiliore et foliis oblique obovatis apice rotundatis longe recedit.

Herba caule ad 10 cm longo erecto vel basi decumbente in siccitate brunneo longitudinaliter rugoso (in vivo subcarnoso?) basi radicante. Folia ut videtur alterna, altero cujusque paris ad auriculam lateralem ca. 2 × 4 mm redacto; petiolus 1–2.5 cm longus, pilis brevibus patentibus indutus; lamina 10–16 × 4–6 cm longa, inaequaliter (subfalcatim) elliptica, acuta vel breviter acuminata, basi inaequilateraliter angustata, marginibus irregulariter acute dentato-serrata, supra glabra in siccitate sclereidis rugulosa, infra ad venas leviter prominentes et ad venulas pilis brevibus saepe hamatis pubescens, venis lateralibus utrinsecus 5–7. Inflorescentia terminalis, simplex vel basi ramo uno praedita, ad 10 cm longa; pedunculus 4–7 cm, dimidio superiore bracteis sterilibus 1–2 ornatus, glaber; pedicelli 0.5–1 cm longi, pilis saepe hamatis breviter pilosi, ebracteati. Calyx ca. 7 mm longus, ad trientem 5-lobus, sinubus conspicue plicatus, extra pilis saepe hamatis indutus, intus brevissime pubescens pilis paucis hamatis. Corolla rotata, ca. 1 cm longa, ad mediam subaequaliter 5-lobata, lobis ca. 5 × 5 mm apice rotundatis marginibus undulatis. Stamina fertilia 4, basi corollae orientia; filamenta filiformia ca. 2 mm longa, glabra; antherae obtuse triangulares, basi leviter cordatae, apicibus cruciatim cohaerentes. Ovarium ovoideo-oblongum, 1.5 mm longum, glabrum, in stylum fere aequilongum robustum parce patenter pubescentem transiens; stigma bilamellatum, marginibus ciliis planis ornatis.

TYPE. Papua New Guinea, West Sepik Prov., Carpentaria Expedition Base Camp, stream margin from K1 to K18 helipad, 340 m alt., January 1978, *W. S. Hoover 832* (A).

ADDITIONAL SPECIMENS. **Papua New Guinea.** WEST SEPIK PROV. Telefomin Subdistr.: Prospect Creek near Frieda R., 4°42′S, 141°48′E, valley forest, 445 m alt., *Henty & Foreman NGF 42601* (L); Carpentaria Expedition Base Camp, stream margin NE of ridge above Storm Creek, 550 m alt., *Hoover 768* (A).

ACKNOWLEDGMENTS

I wish to thank P. F. Stevens (Arnold Arboretum) for making W. Scott Hoover's New Guinea material available to me, and N. P. Balakrishnan (Botanical Survey of India) for the specimen from the Nicobar Islands. I recently visited the Rijksherbarium, Leiden, and I am greatly indebted to the director, C. C. Kalkman, for facilities there. Anton Weber (Vienna) kindly criticized the first draft.

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NOTES ON SALVIA (LABIATAE) IN MEXICO, WITH THREE NEW SPECIES

T. P. RAMAMOORTHY

THE GENUS *Salvia* L., well known to horticulturists, is an outstanding member of the Mexican flora. With its bright red, blue, sometimes yellow, or occasionally white flowers, it is a very conspicuous element in the highlands of Mexico. The flowers range in length from ca. 8 mm (*S. hispanica*) to 6 cm (*S. fulgens*). Common pollinators are hummingbirds, bees, and butterflies. A very high percentage of species are perennials; there are very few annual species of *Salvia* in Mexico.

Standley and Williams (1973) estimated that the genus consists of over 900 species, with nearly 500 from the Americas. Fernald's (1900) synopsis of the Mexican and Central American species of *Salvia* updated Bentham's (1848) and Hemsley's (1882) accounts. Bentham recognized 118 species, Hemsley 126, and Fernald 217.

Epling (1939), perhaps the most distinguished student of the genus, recognized 233 species for Mexico (all belonging to subg. CALOPHACE (Bentham) Epling). Twenty sections and 200 species are endemic to Mexico. In a subsequent series of supplementary notes (1940, 1951, 1957, 1962), he described several more species.

The increase in botanical activity in Mexico during the last few years has resulted in many new specimens that were not available to earlier botanists. I have studied the specimens of *Salvia* among these collections, along with the very rich holdings of the genus in the Gray Herbarium, Harvard University. This is the first report resulting from my study.

It now seems certain that over 275 species of *Salvia* (30 percent of the genus) occur in Mexico; of these, 88 percent (over 26.7 percent of the genus) are endemic to Mexico. Mexico has indeed been a primary center of speciation for *Salvia*.

Three new species are described here. A commentary on *Salvia tubifera* is also provided.

Salvia anastomosans Ramamoorthy, sp. nov. FIGURE 1.

Caulis pilis ramosis adpressis gerens. Foliorum laminae 1.5–3.7 cm longae, 0.5–1 cm latae, oblongae, ad extremos rotundatae, supra glabrae, subtus adpresse albo-tomentosae; venae anastomosantes. Calyx albo-tomentosus, ca. 7.5 mm longus, ca. 3 mm latus. Corolla azurea, ca. 1.2 cm longa.

Erect perennial shrub to 2 m tall, profusely branched. Stem terete, appressed

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FIGURE 1. **Salvia anastomosans** (from holotype): a, habit; b, leaf; c, flower; d, dissected corolla.

white-tomentose with branched hairs when young, becoming glabrous with age. Petiole 0.5–1 cm long, appressed white-tomentose with branched hairs; leaf blade oblong, 1.5–3.7 by 0.5–1 cm, rounded at both ends, entire, glabrous above, appressed white-tomentose beneath with branched hairs, the midrib pronounced, especially beneath, with 9 to 12 pairs of lateral veins, secondary veins numerous and anastomosing into fine network very pronounced against white pubescence. Inflorescences axillary and terminal racemes of interrupted verticils, the internodes separating verticils 0.5–1 cm long, appressed white-tomentose with branched hairs; bracts small, inconspicuous, white-tomentose, early deciduous; pedicels 1–2 mm long, white-tomentose. Calyx ca. 7.5 by 3 mm, bearing numerous sessile glands, these covered by white tomentum of branched hairs, the upper lip entire, acuminate, the lower with 2 acuminate lobes; corolla ca. 1.2 cm long (tube 6 by 3 mm), blue, the upper lip nearly entire, obscurely emarginate, bearded above, as long as lower lip, the lower lip 3-lobed, with lateral lobes shorter and rounded, and middle lobe ca. 6 by 6 mm, broadly rounded, emarginate, undulate; stamens 2, included, filaments 2 mm long, connective ca. 4 mm long, anthers ca. 2 mm long; style ca. 1.4 cm long, slightly exceeding corolla, divided into 2 unequal arms, glabrous.

TYPE. Mexico, Oaxaca, Teposculula, above Tamazulapan (alt. 2250 m), "matorral" with *Bursera,* tree *Ipomoea,* etc., Aug. 8, 1981, *D. Lorence et al. 3709* (holotype, MEXU).

The specific epithet refers to the impressively anastomosing venation pattern that helps to distinguish the species immediately. *Salvia anastomosans* belongs to sect. TOMENTELLAE Epling and is related to *S. candicans,* which differs in having truncate leaf bases and less obvious venation.

Salvia boegei Ramamoorthy, sp. nov. FIGURE 2.

Petioli 2–6 mm longi, prope basin articulati, albo-villosi. Foliorum laminae 1–2.8 cm longae, 0.8–1.9 cm latae, ovatae, ad apicem acutae, ad basim truncatae vel subcordatae, supra puberulae, subtus ad nervos villosae. Verticilli fere capitati 2 cm lati. Calyx albo-lanosus. Corolla azurea, 2–2.1 cm longa, tubo papillato.

Erect perennial shrub or subshrub (height not known), profusely branched. Stem reddish, angled, white-tomentose to villous, glabrous with age. Petiole 0.2–0.6 cm long, articulated near base, white-villous; leaf blade ovate, 1–2.8 by 0.8–1.9 cm, acute at apex, truncate to subcordate at base, crenate-serrate at margin, puberulent above, appressed-villous along nerves beneath and with numerous sessile glands, lateral veins 3 to 5 pairs, secondary veins anastomosing. Inflorescences terminal racemes of interrupted verticils, the internodes separating verticils 1–2.5 cm long, white-villous, the verticils up to 2 cm across, many flowered, crowded into capitula; bracts ca. 5 by 3 mm, ovate, acuminate, early deciduous, villous on back; pedicels 2–3 mm long, white-woolly. Calyx ca. 6 by 4 mm, covered with dense, white wool (wool obscuring lobes), bilabiate, the upper lip entire, rounded, the lower obscurely 3-lobed, with lateral lobes

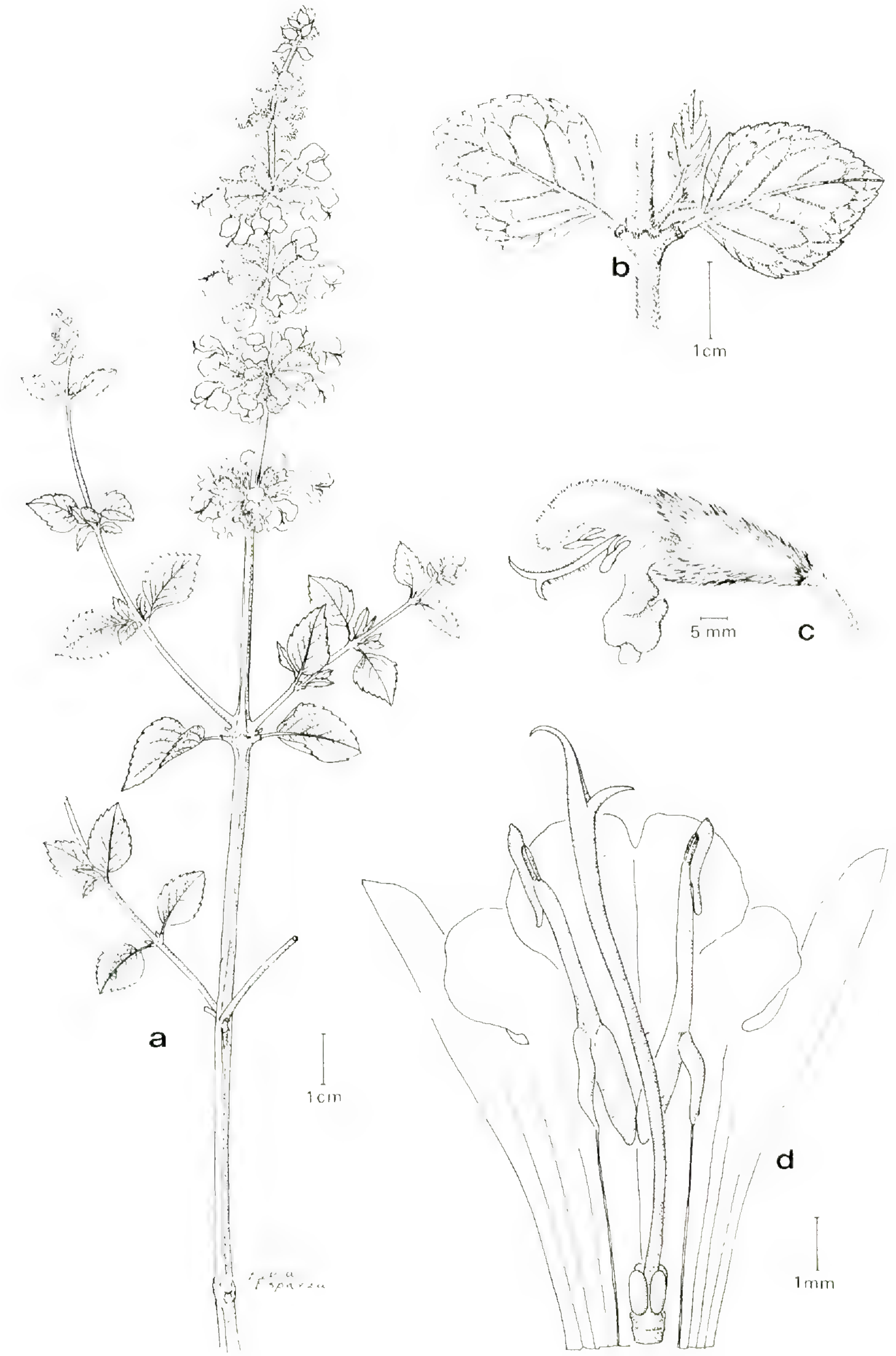


FIGURE 2. **Salvia boegei** (from holotype): a, habit; b, node with leaves; c, flower; d, dissected corolla.

shorter, all rounded; corolla 2–2.1 cm long (tube 6 mm long, with pair of papillae toward base on inside), blue, the upper lip 4.5 mm long, as long as lower, emarginate, bearded on back, bearing many sessile glands, these white when dry, the lower lip ca. 4.5 by 4.5 mm, villous on outside, bearing glands, 3-lobed, with lateral lobes shorter, middle lobe rounded and undulate; stamens 2, included, filaments ca. 2 mm long, connective ca. 3.5 mm long, anthers ca. 2 mm long; style 1.1–1.2 cm long, hairy, barely exserted, divided into 2 unequal arms.

TYPE. Mexico, Puebla, Puente de Dios Molcaxac (alt. 1800 m), with *Dasylirion, Agave, Nolina, Yucca,* Sept. 16, 1971, *W. Boege 1933* (holotype, MEXU).

This species is named after Mr. Wolfgang Boege, an inspiring teacher and plant collector, whose excellent personal herbarium is now with the National Herbarium of Mexico (MEXU). He died in Jalisco in 1975 while on a plant-collecting expedition.

Salvia boegei can be recognized immediately by its articulated petiole, almost capitate verticils, and woolly white calyx. It belongs to sect. SCORODONIA Epling and appears to be related to *S. breviflora,* which differs in having tardily deciduous bracts and leaves that are whitish beneath.

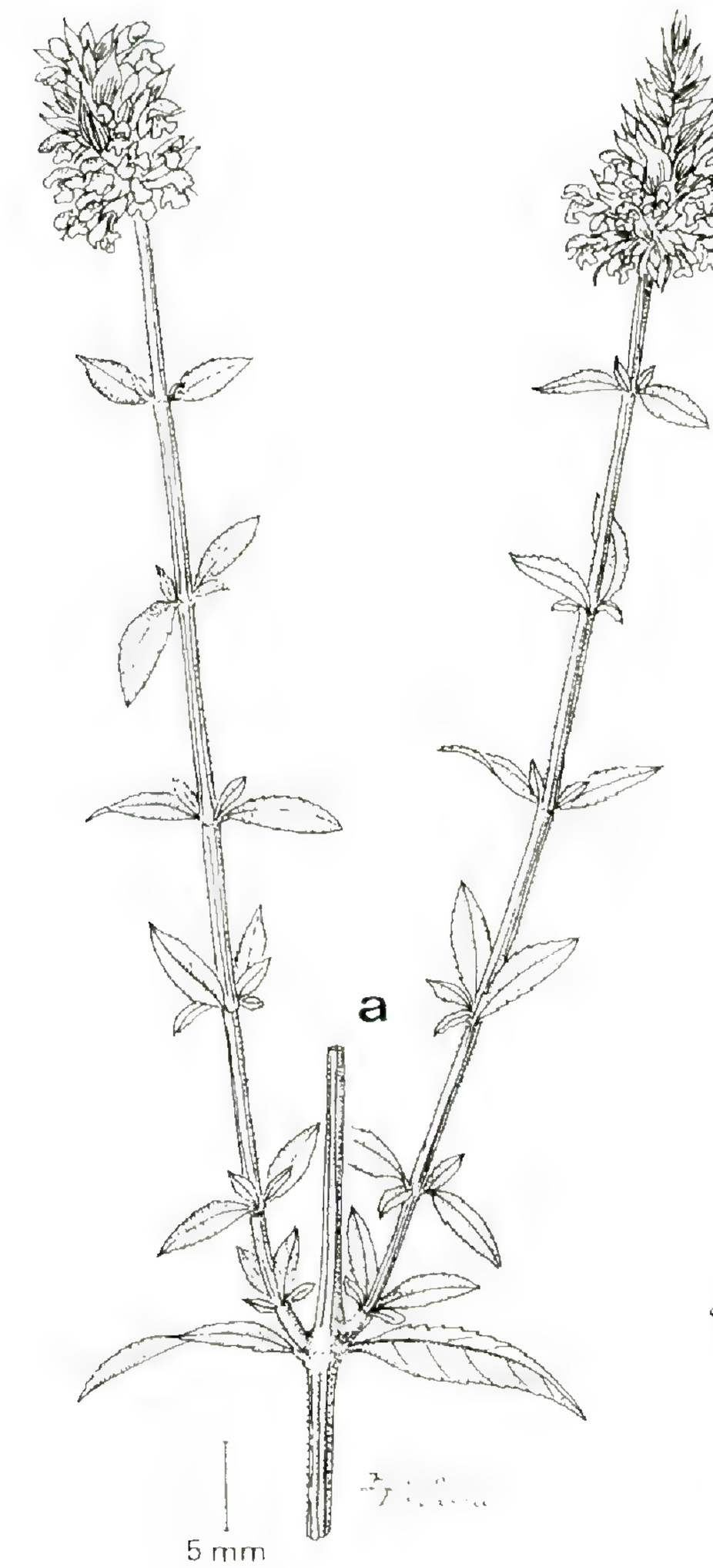
Salvia rzedowskii Ramamoorthy, sp. nov. FIGURE 3.

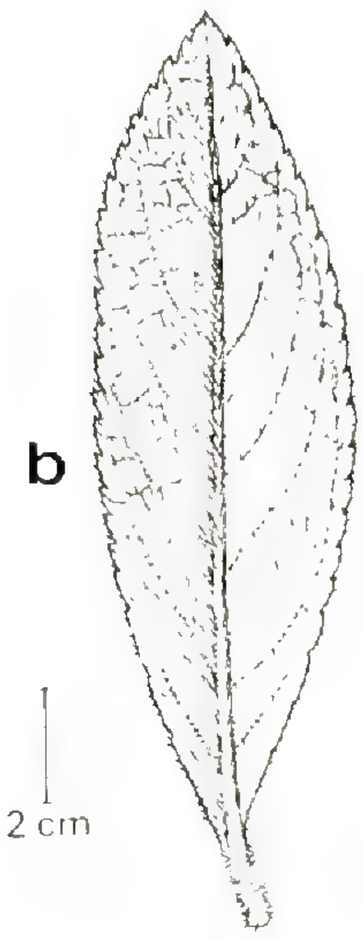
Caulis pilis albis reflexis obsitus. Folia crassa, 2–6 cm longa, 0.6–1.6 cm lata, elliptica, ad basin et ad apicem acuta, supra pilosa, subtus albo-lanata. Verticilli congesti. Calyx villosus, ca. 1.1 cm longus, 2.5 mm latus. Corolla alba, ca. 1.3 cm longa.

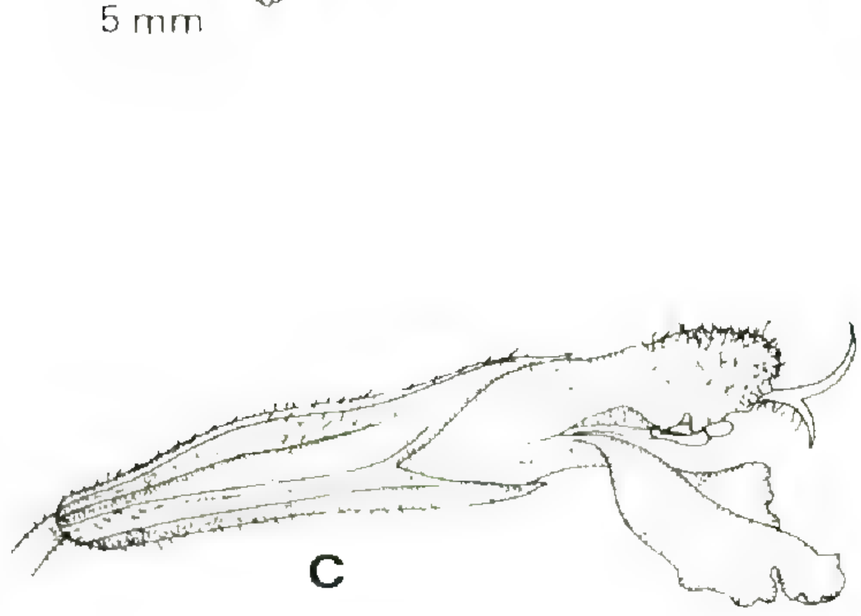
Erect, perennial, suffrutescent herb to 6 dm tall, branched. Stem 4-angled, sulcate, tomentose with white, reflexed hairs, pilose to glabrous with age. Petiole 1–3 mm long, villous; leaf blade thick, elliptic, 2–6 by 0.6–1.6 cm, acute at both ends, crenate-serrate at margin, pilose above, with 6 to 8 pairs of faint lateral veins, white-woolly below. Inflorescences terminal racemes of crowded verticils, internodes separating verticils not well pronounced; bracts small, ca. 1–2 cm by 4 mm, ovate, caudate-acuminate; pedicels 2–4 mm long, terete, villous, spreading at anthesis. Calyx villous, ca. 1.1 cm by 2.5 mm, bilabiate, the upper lip ovate, acuminate, entire, the lower with 2 ovate, acuminate lobes; corolla ca. 1.3 cm long (tube ca. 8 by 2.5 mm, glabrous), white, the upper lip 5 mm long, rounded and emarginate at tip, bearded, the lower lip ca. 6 by 6 mm, 3-lobed, with lateral lobes shorter and rounded, middle lobe undulate; stamens 2, included, filaments ca. 2.5 mm long, connective ca. 2 mm long, anther ca. 2 mm long; style ca. 1.2 cm long, hairy, divided into 2 unequal arms.

TYPE. Mexico, México, 5 km SW of Sultepec, on the road to Amatepec, mesophyllous forests (alt. 2350 m), February 18, 1979, *J. Rzedowski 36071* (holotype, MEXU).

The specific epithet honors Dr. Jerzy Rzedowski, whose contribution to Mexican botany is well known.







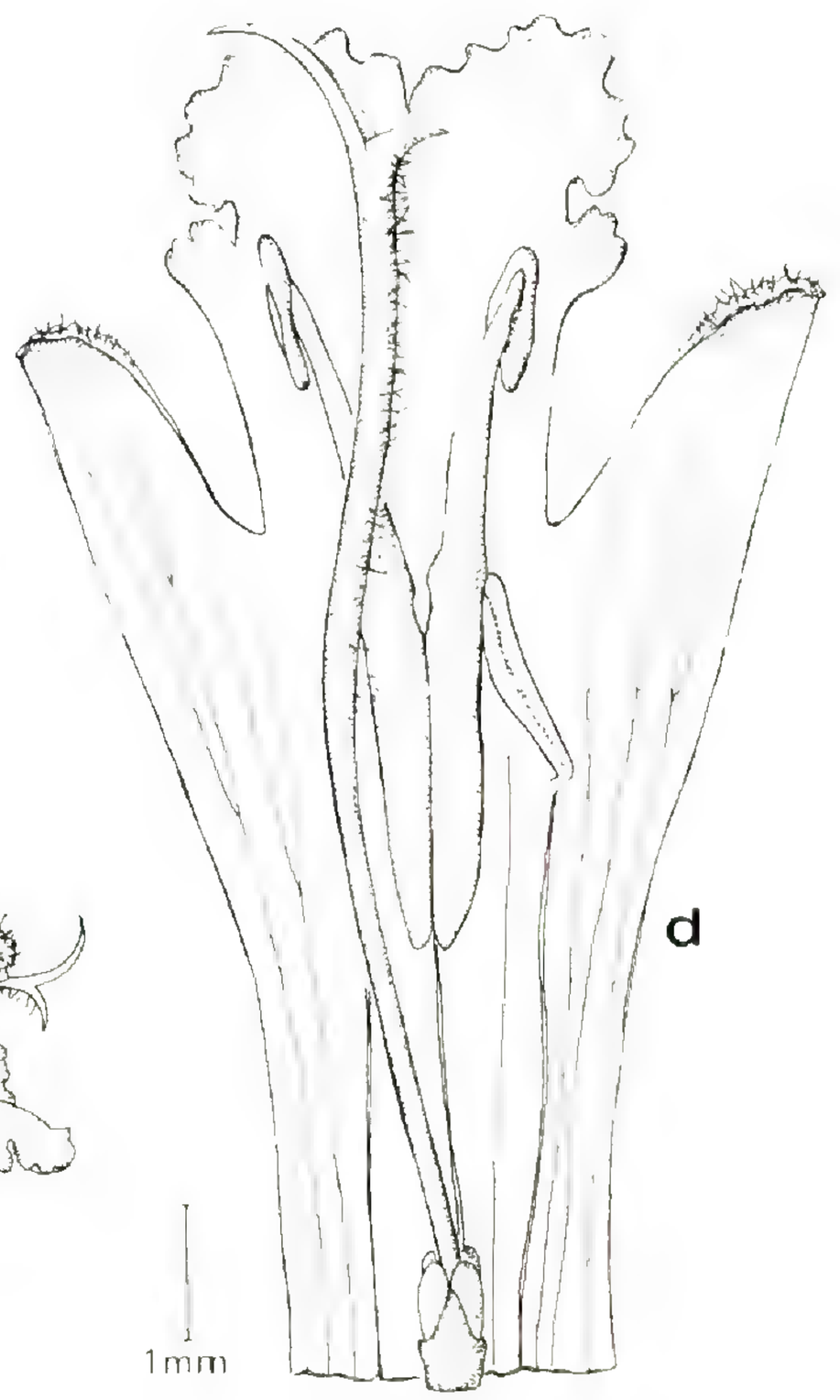


FIGURE 3. **Salvia rzedowskii** (from holotype): a, habit; b, leaf; c, flower; d, dissected corolla.

Salvia rzedowskii is easily recognized by its thick leaves that are white-woolly beneath, its condensed raceme (resembling a nearly cone-shaped head), its caudate-acuminate bracts, and its white flowers. White flowers in *Salvia* are rare, and the species may be moth pollinated. The affinities of this species are not clear.

SALVIA TUBIFERA, A LITTLE-KNOWN SPECIES

Cavanilles (1791) described *Salvia tubifera* from cultivated plants grown from seeds brought from Mexico. No exact locality for the original seed collection is known. Fernald (1900) included this species in his synopsis of Mexican and Central American salvias but did not cite any additional specimens. Epling assigned it to sect. TUBIFLORAE Epling and cited two specimens, one from Real del Monte, Hidalgo, Mexico, and the other from the central valley of Mexico. I have seen both. The species has been re-collected twice from near Real del Monte, in 1950 by Matuda and in 1982 by Benitez. Recent studies have shown that the species is, in fact, widespread and has been going by the names *S. excelsa* and *S. venosa.*

Salvia excelsa was described by Bentham from plants grown from seeds supposedly of Guatemalan origin. I have seen a photograph of the type, old collections in the Gray Herbarium (GH), and recent collections in the Herbario Nacional (MEXU) and the herbarium of the Escuela Nacional de Ciencias Biológicas (ENCB). These clearly match Cavanilles's plate of *S. tubifera* Cav. and the type photo of the species.

Salvia venosa, described by Fernald (1900), is based on a collection from near San Cristóbal las Casas in Chiapas, Mexico (*Nelson 3138* (GH, US)). Epling (1939) separated *S. venosa* and *S. excelsa* on geographic grounds (Chiapas vs. Guatemala) but later (1940) concluded that they were conspecific. I have seen the type material at GH and am of the same opinion. These plants that have been going by three different names represent only one species, for which the earliest name is *S. tubifera* Cav.

Complete specimen citation with synonymy and a description are provided here.

Salvia tubifera Cav. Ic. Descr. Pl. **1:** 16. *t. 25.* 1791 (illustration and description of plants grown from seeds brought from Mexico). LECTOTYPE: we have recently received in MEXU photographs of types of all salvias in the collections at MA described by Cavanilles. There are two specimens labeled *S. tubifera,* and I designate the specimen with the annotation "*S. tubifera* Icon. t. 25" as lectotype. Epling did not typify the name in 1939.

Salvia longiflora Willd. Sp. Pl. **1:** 141. 1797, nom. superfl. TYPE: Willdenow cited a "specim. verum in herb. Jussieu vidi"; this may be considered as the type of his binomial.

Salvia excelsa Bentham, Bot. Gaz. **27:** 90. 1841. TYPE: description from plants grown from seeds brought from ?Guatemala (holotype, specimen in K, n.v., photo GH!).

Salvia venosa Fern. Proc. Amer. Acad. Arts **35:** 545. 1900. TYPE: Mexico, Chiapas, San Cristóbal las Casas, *Nelson 3138* (holotype, GH!; isotype, US!).

Herb or subshrub 0.5–1.2 dm tall, branched. Stem 4-angled, sulcate, villous when young, sparsely pilose to glabrous with age, the hairs multicellular, often crisped, usually appressed, often persisting along grooves. Petiole 2–5 cm long, villous, the hairs usually crisped; leaf blade ovate, sometimes nearly rotund-ovate, 4–12 by 2.5–7.1 cm, apex acute to acuminate, base broadly to narrowly cuneate to somewhat truncate, margin crenate-serrate, lateral veins 4 to 7 pairs, upper surface pilose to glabrescent, lower surface densely to moderately villous to nearly glabrescent and paler. Inflorescences terminal racemes of interrupted, 2- to 6-flowered verticils separated by internodes of 0.5–4 cm; bracts 4 mm–1.2 cm by 4–8 mm, broadly ovate, caudate-acuminate, pilose abaxially, early deciduous; pedicels 1.5–8 mm long, angled, villous. Calyx 8 mm–1.1 cm by 3–4 mm, pilose to glabrous above, usually villous to hispid below, bilabiate, upper lip entire, lower 2-lobed, all acuminate; corolla 2.6–3 cm long (tube 2.2–2.4 cm by 3–4 mm), scarlet, villous, the upper lip 5–6 mm long, longer than lower, rounded, emarginate, enclosing stamens and stigma, the lower lip 3–4 by 3–4 mm, 3-lobed, with lateral lobes shorter, middle lobe larger and rounded, all reflexed; stamens 2, the filaments 3 mm long, attached near base of corolla tube, the connective 2–2.2 cm long, the anthers 2.7 by 0.5 mm, acute at ends; style as long as corolla tube, pilose, ending in 2 unequal stigmatic lobes. Seeds not seen. Flowering July to November.

DISTRIBUTION. Nuevo León in northern Mexico (Epling (1951) cited *Meyer & Rogers 2891* from Nuevo León, but I have not seen it) through Hidalgo, Puebla, Guerrero, and western Veracruz to Chiapas and ?Guatemala in the southeast. Usually in pine/oak forests; 1800–2750 m alt.

SPECIMENS EXAMINED. **Mexico.** HIDALGO: Zimapán, between Zimapán and Jacala, Barranca de San Vicente, near km 238, *Moore & Wood 4435* (GH), *Moore & Wood 5065* (GH, MEXU); Real del Monte, *Matuda 18883* (MEXU); Zempoala, *Benitez 836* (ENCB, MEXU). PUEBLA: Puebla-Veracruz border, Cumbres de Aculcingo, *Boege 1953* (GH, MEXU). VERACRUZ: Puerto del Aire, *Rosas 802* (GH, MEXU); El Puerto, *Sharp 44703* (MEXU). GUERRERO: Omiltepec, *Halbinger s.n.*, November, 1975 (MEXU). CHIAPAS: San Cristóbal las Casas, *Breedlove 11903* (MEXU), *Ghiesbreght 749* (GH). Without definite locality,[1] *Coulter 1088, 1089* (GH).

This widespread but rare, moderate-sized, scarlet-flowered *Salvia* is one of the numerous attractive species in Mexico. Plants from Veracruz are glabrescent, those of Puebla and Hidalgo very pubescent, and those of Guerrero intermediate. The number of flowers is variable: plants from Hidalgo and Chiapas bear more than do those of Puebla, Veracruz, and Guerrero.

Epling (1939) classified *Salvia tubifera* Cav. (including *S. longiflora* Willd.) in sect. TUBIFLORAE Epling, and *S. venosa* and *S. excelsa* in sect. CURTIFLORAE

[1]I do not know the definite localities for these two numbers. Fernald (1900) referred them to Zempoala in Hidalgo (Real del Monte is in Municipio Zempoala). Epling (1939), however, thought that one came from the Valley of Mexico, and the other from Real del Monte; he did not say which number was from where.

Epling. In general morphology *S. tubifera* resembles *S. nervata* Martens & Gal. of sect. CURTIFLORAE more than it does any members of sect. TUBIFLORAE.

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CUBITANTHUS, A NEW GENUS OF GESNERIACEAE FROM BRAZIL

KERRY BARRINGER

RUSSELIA ALATA Cham. & Schlecht. was originally assigned to the Scrophulariaceae and was included as such in the *Flora Brasiliensis* (Schmidt, 1862). Bentham (1846) noted that this species was not a *Russelia* L. f. but did not suggest an alternative placement until 1876, when he included it under *Anetanthus* Hiern (Gesneriaceae) in *Genera Plantarum*. In all, Bentham included four species in *Anetanthus*; of these, Howard (1975) retained *A. gracilis* Hiern and *A. alatus* (Cham. & Schlecht.) Durand & Jackson and transferred the others to different genera. Wiehler (1976) also reviewed the genus but found little relationship between *A. gracilis* and *A. alatus*. He retained *A. gracilis* in a monotypic *Anetanthus* to which Skog (1982) has only recently added a second species. Wiehler rejected *A. alatus* as a gesneriad and suggested that it be placed somewhere in the Scrophulariaceae. Although Wiehler cited the type at Kew (*Sellow s.n.*), it appears that most of his observations are based on a plate published by Schmidt (1862) that misrepresents critical features of the species: the nectary is omitted, the placentation is shown as axile, and the seeds appear angular.

Dr. Mattos Silva, of the Centro de Pesquisas do Cacau (CEPEC), has recently made material of this rarely collected species available to me. Study of these specimens confirms Bentham's contention that the species should be included in the Gesneriaceae but shows that it is distinct from *Anetanthus* and merits generic status.

Cubitanthus Barringer, gen. nov.

Herbae decumbentes pilosae, caules alati, radices fibrosae saepe adventitiae. Folia opposita petiolata serrata nervis pinnatis. Flores solitarii axillares ebracteolati, calyx quinquelobus lobis liberis lanceolatis acutis interne glabris, corolla quinqueloba bilabiata labio superio subintegro labio inferno trilobo ad basem villoso, stamina 4 geniculata, antheris cohaerentibus, discus integer, ovarium superum uniloculare placentatione parietali. Capsula septicida bivalvata, semina obovoidea striata.

Decumbent herb with long multicellular hairs; stem 4-winged; roots fibrous, often adventitious. Leaves opposite; petiole slightly winged; blade serrate, venation pinnate. Flowers solitary in leaf axils; pedicel slightly winged at base, ebracteolate; calyx 5-lobed to base, the sepals lanceolate, acute, adaxially gla-

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brous; corolla cylindrical, 5-lobed, bilabiate, the upper lip subentire, not reflexed, the lower lip 3-lobed, densely villous at base; stamens 4, geniculate, adnate to base of corolla, the anthers bilocular, coherent in pairs; disc entire, annular; ovary superior, the placentation parietal, the style elongate, the stigma entire and slightly enlarged. Capsule septicidal, 2-valved, included within persistent calyx. Seeds ovoid, slightly striate.

TYPE. *Cubitanthus alatus* (Cham. & Schlecht.) Barringer.

ETYMOLOGY. From the Greek *kubitos*, bearded, and *anthos*, flower, in reference to the densely villous lower lip of the corolla.

Cubitanthus alatus (Cham. & Schlecht.) Barringer, comb. nov.

Russelia alata Cham. & Schlecht. Linnaea **3:** 3. 1828. TYPE: Brazil, *loc. ignot.*, *Sellow s.n.* (holotype, B (destroyed); lectotype (here designated), K!).
Anetanthus alatus (Cham. & Schlecht.) Bentham & J. D. Hooker ex Durand & Jackson, Index Kew. **1:** 133. 1893.

SPECIMENS EXAMINED. **Brazil.** BAHIA: Itabuna, Ilheus, CEPEC, regiao de Mata Higrophila Sul Baiana, 15 Sept. 1981, *Hage, Brito, & Argolo 1328* (CEPEC, F); Itajuipe, San Antonio, 18 km do S de Itajuipe, 3 Feb. 1970, *Dos Santos 554* (CEPEC, F).

Cubitanthus alatus is found as a weed in cacao plantations, but is known only from the cities of Ilheus and Itajuipe in Brazil. It seems likely that it will be found more extensively in the coastal forest zone. The lectotype lacks locality data, as is typical of specimens collected by Sellow, but Urban (1906) reported that Sellow had collected in the coastal forests of Bahia in 1817 and it is likely that the specimen was collected at that time.

The parietal placentation, disc, coherent anthers, and striate seeds are sufficient to place *Cubitanthus* in the Gesneriaceae. While these characters are also found in the Scrophulariaceae, they never occur in combination with each other. Both *Anetanthus* and *Cubitanthus* are decumbent herbs with entire discs and septicidal capsules. *Anetanthus* differs in having flowers in long-pedunculate cymes, glandular-pilose calyxes that also have short glandular hairs on their inner surfaces, a bilobate upper corolla lip, stomatomorphic stigmas, and flattened, winged seeds. *Cubitanthus* is unique in having a winged stem and a densely bearded lower corolla lip. Both *Cubitanthus* and *Anetanthus* are best assigned to the Beslerieae *sensu* Wiehler (1976).

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FRUITS AND SEEDS OF THE CUNONIACEAE

WILLIAM C. DICKISON

THE DICOTYLEDONOUS FAMILY Cunoniaceae consists of woody plants almost totally restricted to the Southern Hemisphere. It has long been of evolutionary interest as a putatively primitive and basal or near-basal group in the large rosalean complex from which a number of families have perhaps been derived (Dickison, 1975a). Depending upon taxonomic interpretation, it contains between 19 and 27 genera.

As pointed out by Dickison (1980b), members of the family are morphologically diverse, and considerable difference of opinion still exists regarding both generic circumscription and intrafamilial and interfamilial relationships. For example, an overall similarity in gross floral morphology has recently led Hoogland (1979) to reduce four Australasian genera to synonymy with the previously monotypic Chilean genus *Caldcluvia* D. Don and, at the same time, to establish the new segregate genus *Acsmithia* Hoogl. Within the family, Engler (1928), in his treatment for *Die Natürlichen Pflanzenfamilien,* recognized 26 genera distributed among five tribes. These five tribes have been maintained by Schulze-Menz (1964) in the most recent edition of Engler's *Syllabus.* Available evidence indicates, however, that Engler's treatment does not accurately reflect evolutionary groupings within the assemblage.

It is becoming clear, moreover, that parallel and reticulate evolution have often produced superficially similar morphologies among cunoniaceous genera. It is equally clear that the previously available morphological and anatomical data have often led to inaccurate systematic conclusions. During the past several years, I have been engaged in a thorough morphological and anatomical study of the Cunoniaceae with three main objectives: a better circumscription of the family and an eventual clarification of the interrelationships among genera of Cunoniaceae; an elucidation of the relationships of the Cunoniaceae to other families; and a better understanding of the overall patterns and trends of evolution within the family. Toward these goals, earlier research has dealt with aspects of floral (Dickison, 1975a), foliar (Dickison, 1975b), nodal (Dickison, 1980a), and wood anatomy (Dickison, 1980b). Although the resulting data

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have provided further insight into the relationships and relative degrees of advancement of various taxa, additional detailed and comprehensive study of other aspects will be required in order to obtain a reasonably accurate picture of intrafamilial relationships. This paper describes the anatomy of both fruits and seeds.

The very scanty embryological information available on the Cunoniaceae has been summarized by Davis (1966). Aside from the incomplete accounts provided in numerous regional floras, little has been written concerning fruit and seed structure of the family (see Corner, 1976). More recent contributions dealing with cunoniaceous embryology and seed structure include papers by Govil and Saxena (1976) on *Weinmannia fraxinea,* Prakash and McAlister (1977) on *Bauera capitata* Ser., Krach (1977) on general seed morphology in the Cunoniaceae, and Kennedy and Prakash (1981) on *Callicoma serratifolia.* Outline drawings of seeds were provided by Bernardi (1964) in his revision of *Weinmannia.*

MATERIALS AND METHODS

Fruits and seeds of 20 genera and close to 100 species were examined in the present study. Specimens studied are presented in TABLE 1. Preserved fruits and seeds, in various stages of maturation, were embedded in paraffin and cut on a rotary microtome. Sections were subsequently stained with a combination of safranin and fast-green. Additional seeds were gathered from mature fruits on herbarium specimens housed at A, BRI, CANB, DUKE, GH, L, NCU, NOU, and Z (herbarium acronyms according to Holmgren, Keuken, & Schofield, 1981). For scanning electron microscopy, dried seeds were affixed to stubs with double-stick tape, gold coated, and observed directly. The concept used of familial and generic limits follows Hoogland (1960, 1979, 1981). Most seed terminology follows the usage of Corner (1976). Slides are deposited in the Department of Biology, The University of North Carolina at Chapel Hill.

OBSERVATIONS

DEHISCENT-FRUITED GENERA

FRUITS. Twelve genera are characterized by dehiscent fruits: *Acrophyllum* Bentham (1 species), *Acsmithia* (14), *Bauera* Banks ex H. C. Andrews (3), *Caldcluvia* (11), *Callicoma* H. C. Andrews (1), *Cunonia* L. (ca. 20), *Geissois* Labill. (ca. 17), *Lamanonia* Vell. (6 to 8), *Pancheria* Brongn. & Gris (ca. 28), *Spiraeanthemum* A. Gray (6), *Vesselowskya* Pampan. (1), and *Weinmannia* L. (ca. 150). Fruits and seeds of *Bauera* were the only ones not examined.

In *Acsmithia* and *Spiraeanthemum* each carpel of the apocarpous gynoecia matures into a follicular fruit (FIGURE 1), while all other genera produce two-(to five-)valved, sometimes horned capsules that undergo septicidal dehiscence (FIGURES 2, 4–7). In contrast with the capsules of other genera, those of *Cunonia* dehisce by means of an acropetal separation of carpels from the persistent central column of tissue (FIGURE 3). Fruit-wall surfaces range between glabrous

TABLE 1. **Specimens of Cunoniaceae examined.**

TAXON	COLLECTOR	COUNTRY OF ORIGIN	VOUCHER	FRUIT	SEED
Acrophyllum australe (A. Cunn.) Hoogl.	Stauffer et al. 5700	Australia	A	+	+
Acsmithia densiflora (Brongn. & Gris) Hoogl.	McKee 2683	New Caledonia	L		+
	Dickison 220	New Caledonia	NCU	+	+
	Musselman et al. 522	New Caledonia	NCU		+
	Stauffer et al. 5797	New Caledonia	Z		+
A. elliptica (Pampan.) Hoogl.	Veillon 2844	New Caledonia	NCU		+
A. integrifolia (Pulle) Hoogl.	Brass 12693	New Guinea	L		+
A. pedunculata (Schlechter) Hoogl.	Veillon 1079	New Caledonia	NOU		+
A. pubescens (Pampan.) Hoogl.	Schmid 431	New Caledonia	NOU		+
A. pulleana (Schlechter) Hoogl.	Brass 12017	New Guinea	A, L		+
A. reticulata (Schlechter) Hoogl.	Galore & Wood, NGF 41005	New Guinea	A, L		+
A. undulata (Vieill.) Hoogl.	Vieillard 2078	New Caledonia	L		+
Aistopetalum multiflorum Schlechter	Hoogland & Craven 10826	New Guinea	CANB	+	+
Anodopetalum biglandulosum (Hooker) Hooker f.	Webb 3337	Tasmania	BRI	+	+
Caldcluvia australiensis (Schlechter) Hoogl.	Hoogland 8538	Australia	A, L	+	+
C. brassii (Perry) Hoogl.	Brass 30592	New Guinea	L		+
	Brass 29616	New Guinea	A		+
	Hoogland [illegible]	New Guinea	CANB	+	+
C. celebica (Blume) Hoogl.	Hartley 12298	New Guinea	L		+
	Havel & Katz, NGF 17084	New Guinea	A		+
	Brass [illegible]	Solomon Is.	BRI		+
	K[illegible]jewski [illegible]	Bougainville Is.	BRI		+
C. clemensiae (Perry) Hoogl.	Van Balgooy 969	New Guinea	L		+
C. fulva (Schlechter) Hoogl.	Van Royen, NGF 18266	New Guinea	L		+
C. nymanii (K. Schum.) Hoogl.	Henty et al., NGF 41525	New Guinea	L		+
	Stevens, LAE [illegible]3	New Guinea	L		+
	Hoogland & Schodde 7325	New Guinea	Z		+
	Hoogland & [illegible] et al. 69	New Guinea	L	+	+
	Croft & Isbell, [illegible]981	New Guinea	A	+	+
C. paniculata (Cav.) D. Don	Dombey 713	Chile	L		+
	Eyerdam & Beetle 24618	Chile	GH		+
C. paniculosa (F. Mueller) Hoogl.	Thorne et al. 25938	Australia	L		+
	Hoogland 1115	Australia	CANB		+
C. papuana (Pulle) Hoogl.	Kalkman 5316	New Guinea	L		+
C. rosifolia (A. Cunn.) Hoogl.	Wilkes Exp. s.n.	New Zealand	GH		+
	Walker s.n.	New Zealand	GH		+
C. rufa (Schlechter) Hoogl.	Hoogland & Pullen 6081	New Guinea	L		+
	Hoogland & Pullen 5438	New Guinea	CANB		+
Callicoma serratifolia R. C. Andrews	Hoogland 11692	Australia	A, CANB	+	+
	[illegible] 295	Australia	BRI, NCU	+	+
	White 10279	Australia	A		+
Ceratopetalum succirubrum C. T. White	Hartley 10,967	New Guinea	A	+	+
	Croft & Marsh, LAE 71177	New Guinea	BRI	+	+
Codia nitida Schlechter	Dickison 221	New Caledonia	NCU	+	+
	Jaffre 2223	New Caledonia	NOU		+
C. obcordata Brongn. & Gris	Guillaumin & Baumann-Bodenheim 13117	New Caledonia	A		+
Cunonia atrorubens Schlechter	Blanchon 649	New Caledonia	NOU		+

TABLE 1 (*continued*).

TAXON	COLLECTOR	COUNTRY OF ORIGIN	VOUCHER	FRUIT	SEED
C. balansae Brongn. & Gris	Dickison 230	New Caledonia	NCU	+	+
C. capensis L.	Lam & Meeuse 4656	South Africa	L		+
C. lenormandii Pampan.	McKee 7975	New Caledonia	L		+
C. macrophylla Brongn. & Gris	Bernardi 9507	New Caledonia	L		+
	Webster & Hildreth 14493	New Caledonia	GH	+	
C. pseudoverticillata Guillaumin	McKee 4410	New Caledonia	L		+
C. pterophylla Schlechter	Dickison 238	New Caledonia	NCU	+	+
C. pulchella Brongn. & Gris	Dickison 287	New Caledonia	NCU	+	+
	Dickison 218	New Caledonia	NCU	+	+
C. purpurea Brongn. & Gris	Dickison 156	New Caledonia	NCU	+	+
	Dickison 144	New Caledonia	NCU		+
C. schinziana Däniker	McKee 23112	New Caledonia	NOU		+
Geissois benthamiana F. Mueller	Forest Guard, Lismore 3.1909	Australia	L		+
G. biagiana (F. Mueller) F. Mueller	Dockrill 34	Australia	L		+
G. hippocastaneifolia Guillaumin	Dickison 284	New Caledonia	NCU	+	+
G. pruinosa Brongn. & Gris	Dickison 217	New Caledonia	NCU	+	+
G. stipularis A. C. Sm.	Fiji Herb. 31297	Fiji	NCU	+	+
Gillbeea papuana Schlechter	Brass 31815	New Guinea	A	+	+
Lamanonia ternata Vell.	Irwin et al. 8603	Brazil	GH		+
L. tomentosa (Cambess.) O. Kuntze	Balansa 4752	Paraguay	L		+
Pancheria confusa Guillaumin	Veillon 66	New Caledonia	NOU		+
P. elegans Brongn. & Gris	Dickison 158	New Caledonia	NCU	+	+
P. hirsuta Vieill.	Dickison 227	New Caledonia	NCU	+	+
P. reticulata Guillaumin	Bernardi 12768	New Caledonia	Z		+
P. robusta Guillaumin	Dickison 248	New Caledonia	NCU	+	+
P. sebertii Guillaumin	Franc 2109	New Caledonia	A		+
Platylophus trifoliatus (Thunb.) D. Don	Bolus 621	S. Africa	A	+	+
	Wicht 460/461	S. Africa	L		+
Pseudoweinmannia lachnocarpa (F. Mueller) Engler	Clemens 43294	Australia	A	+	+
Pullea glabra Schlechter	Brass 31156	New Guinea	A	+	+
P. stutzeri (F. Mueller) Gibbs	Irvine 1253	Australia	BRI		+
Schizomeria ilicina (Ridley) Schlechter	Brass 12150	New Guinea	A	+	
S. ovata D. Don	Hoogland 11684	Australia	CANB	+	+
	Dickison & Jessup 297	Australia	BRI, NCU	+	+
S. whitei Mattf.	Dickison 205	Australia	NCU	+	+
Spiraeanthemum katakata Seem.	A. C. Smith 4371	Fiji	A		+
	A. C. Smith 4409	Fiji	L		+
S. macgillivrayi Seem.	Morrison 25.6.1896	New Hebrides	A	+	
S. samoense A. Gray	Bristol 2136	Samoa	L		+
Vesselowskya rubifolia (F. Mueller) Pampan.	White 11482	Australia	A		+
	Schodde 3210	Australia	CANB	+	+
	Herb. D'Alleizette 2151	Australia	L		+
Weinmannia affinis A. Gray	A. C. Smith 7608	Fiji	L		+
W. aphanoneura Airy Shaw	Ashton, BRUN 1044	Borneo	L		+
W. bangii (Rusby) Pampan.	Buchtien s.n.	Bolivia	L		+

TABLE 1 (*continued*).

TAXON	COLLECTOR	COUNTRY OF ORIGIN	VOUCHER	FRUIT	SEED
W. blumei Planchon	Dickison 215	New Guinea	NCU	+	+
	Koorders 7647B	Java	L		+
	Schmutz 4588	Lesser Sunda Is.	L		+
W. celebica Koord.	Van Balgooy 3809	Celebes	L		+
W. clemensiae Steenis	J. & M. S. Clemens 50877	Borneo	L		+
W. decora Tul.	Bernardi 11961	Madagascar	L, Z		+
W. denhamii Seem.	Bernardi 13258	New Hebrides	L		+
	Bernardi 12986	New Hebrides	P		+
W. descombesiana Bernardi	Eyma 3590	Celebes	L		-
W. dichotoma Brongn. & Gris	Bernardi 12616	New Caledonia	Z		+
W. fraxinea (D. Don) Miq.	Forman 51	Cult., Java	L		+
W. glabra L.	Lansberger s.n.	Venezuela	L		+
W. hutchinsonii Merr.	Mendoza, PNH 18409	Philippines	L		+
W. luzoniensis Vidal	Gacad, FB 27274	Philippines	BO		+
W. mauritiana D. Don[1]	D'Alleizette 2166	Réunion	L		+
W. monticola Daniker	McKee 23892	New Caledonia	NOU		+
W. negrosensis Elmer	Ramos, Philippine Plants 1287	Philippines	L		+
W. paitensis Schlechter	Bernardi 9881	New Caledonia	L		+
W. parviflora Forster	Gillett 2215	Marquesas Is.	L		+
W. pinnata L.	Sousa & Rico 8118	Mexico	NCU		+
W. pullei Schlechter	Hoogland & Schodde 7242	New Guinea	Z		+
W. purpurea Perry	Kajewski 1738	Solomon Is.	L		+
W. racemosa L. f.	Philipson et al. 349	New Zealand	NCU		+
	Dickison s.n.	Cult., E		+	+
W. richii A. Gray	A. C. Smith 6813	Fiji	L		+
W. rubrinervis Ettingsh.[2]	D'Alleizette s.n.	Madagascar	L		+
W. serrata Brongn. & Gris	Bernardi 12816	New Caledonia	L		+
W. subsessiliflora Ruiz & Pavon	Vasquez A130	Peru	DUKE		+
W. sylvicola A. Cunn.	Van Steenis 22314	New Zealand	L		+
W. tannaensis Guillaumin	Bernardi 12909	New Hebrides	L, Z		+
W. tinctoria Sm.	Bernardi 14516	Réunion	Z		+
W. trichophora Perry	Pullen 374	New Guinea	L		+
W. trichosperma Cav.	Zollner 3137	Chile	L		+
W. vescoi Drake	Van Balgooy 1796	Tahiti	L		+

[1]Syn. W. biviniana Tul.
[2]Syn. W. rutenbergii Engler.

and tomentose. The calyx is either persistent or deciduous in the fruit, with both of these character states sometimes present within a single genus (e.g., *Weinmannia*).

All of the plants have mature pericarps that are differentiated into an outer parenchymatous region and an inner region of rigid, thick-walled, and highly lignified cells (FIGURES 19, 20, 22). The endocarp tissue is thicker along the

dorsal wall and becomes thinner in ventral regions. In older fruits of *Cunonia,* the endocarp may become separated from the outer parenchymatous layers. The lignified valve margins, which represent the halves of the original septa, are illustrated in FIGURES 2 and 5. Pericarp thickness ranges from a low of four to eight cells (*Weinmannia*) to a high of 30 to 40 cells (*Geissois*). Fruit vasculature mirrors the pattern of gynoecial venation (Dickison, 1975a), although in the mature fruit veins become ensheathed by sclerenchyma.

Epidermal cells of the outer surface of the pericarp are generally rectangular in transection, with a moderately thick cuticle on the outside. *Weinmannia racemosa* has a conspicuously striate external pattern. Mature fruits of *Cunonia pulchella* are covered with six or seven layers of periderm and have scattered lenticels. The parenchymatous central region of the pericarp is composed of isodiametric cells that may become moderately thick walled in older fruits. Numerous brachysclereids are present in the mesocarp. Scattered "mucilaginous idioblasts" with frothy contents occur in *C. balansae, C. pterophylla, Geissois hippocastaneifolia,* and *Pancheria confusa.* Druses are common in *Cunonia balansae, C. capensis, C. pterophylla,* and *Pancheria robusta.* In *Acsmithia densiflora, Caldcluvia rosifolia, Geissois pruinosa, Pancheria gatopensis* Vieill. ex Guillaumin, and *Vesselowskya rubifolia* such crystals are confined to the boundary cells between outer parenchyma and endocarp or to the septum. In some species of *Cunonia,* zonation is indicated in the parenchymatous region of the pericarp by peripheral cells that stain more darkly.

The inner, multiseriate sclerenchymatous region of the fruit wall, which becomes prominent following fertilization, is composed of two distinct zones of variable thickness in which the elongated cells are oriented in opposite planes: cells of the outer zone are arranged with their long axes parallel to the long axis of the fruit, while those of the inner zone are at right angles.

DEVELOPMENT OF THE SEED COAT. Seed coats at early stages of development were examined for a number of capsular cunoniaceous taxa, including *Cunonia balansae* (FIGURE 131) and *Pancheria robusta* (FIGURE 134). Mature ovules are anatropous, bitegmic, and as far as is known, crassinucellate (Davis, 1966). At an early stage of seed-coat development, the outer integument is composed of a tanniferous outer epidermis and one or two subdermal layers consisting of smaller, nucleated, less densely staining cells. The outer epidermis of the inner integument gradually becomes transformed into a sclerotized exotegmen in the mature seed coat; during early stages of development, this layer is composed of rather small, nontanniferous cells with prominent nuclei (FIGURES 131, 134). Although distinction between outer and inner integuments is typically lost in the mature seed coat, examination of developmental stages during seed-coat maturation shows that seeds of the Cunoniaceae are exotegmic (*sensu* Corner, 1976); that is, the outer epidermis of the inner integument differentiates into the mechanical layer. The middle two to four layers of the inner integument, some of which may arise by secondary periclinal divisions, consist of comparatively enlarged, nontanniferous or tanniferous cells that are often tangentially flattened. Additional layers may develop along the seed edges. The inner epidermis is typically made up of densely cytoplasmic, tannin-accumulating

cells that undergo little enlargement. In older seeds the inner epidermis always stains very darkly (FIGURE 133).

MATURE SEEDS. The taxonomic literature indicates that seeds range in length from small (ca. 0.4 mm) to relatively large (ca. 6 mm). I have found no exceptions to these dimensions. Outline varies from narrowly elliptic to elliptic or lanceolate. Angular seeds occur in *Cunonia* (FIGURES 44, 51). Seed numbers range from one to many per locule, with ovule abortion common (FIGURES 130, 132). In cunoniaceous seeds the major features that show significant variation and that may be combined in different ways are type and distribution of epidermal appendages, shape and wall characteristics of epidermal cells, and occurrence, type, and abundance of warts and striations. Seed coats are either glabrous or papillate (tuberculate), and appendages are usually present in the form of wings or hairs. A hilar scar is clearly visible in most taxa (FIGURE 91), and an elongate raised raphe is generally present. Seeds are supplied by a single undivided raphal bundle (FIGURE 135). A straight embryo is always embedded in abundant starchy endosperm (FIGURES 135, 136).

Wings occur on seeds of all examined specimens of *Acsmithia, Callicoma, Cunonia, Geissois, Lamanonia, Pancheria, Spiraeanthemum,* and *Vesselowskya,* as well as on those of some specimens assigned to the genus *Caldcluvia.* Wings are without vasculature and vary in size, shape, and location. Those of *Geissois* are long, flattened structures confined to an upper terminal position on the seed (FIGURE 37). The same condition is found in some species of *Pancheria,* such as *P. confusa* (FIGURES 31, 32), and in *Acsmithia vitiense* (A. Gray) Hoogl. Terminal wings attached both chalazally and micropylarly—and also sometimes laterally—occur in *Acsmithia, Caldcluvia, Cunonia, Lamanonia, Spiraeanthemum, Vesselowskya rubifolia,* and some species of *Pancheria* (FIGURES 33, 39, 46, 49, 52, 55, 57, 58, 65, 71, 73, 81). When both distal and basal wings are present, the two often differ in length and shape. In a number of species of *Acsmithia, Cunonia, Lamanonia,* and *Pancheria,* wings sometimes extend along one or both sides of the seed body as lateral appendage(s) (FIGURES 35, 39, 49, 51, 55). Such lateral wings may extend up to the entire length of the seed body and appear always to form on the hilar side. Wing size and shape are also quite variable, ranging from rather long, broad structures with rounded apices, to triangular, to short, narrow outgrowths. Structurally mature wings consist primarily of two epidermal layers; between these one to three layers of unorganized or crushed cells may occur.

Hairy seeds characterize the large and widely distributed genus *Weinmannia* and the New Zealand and Australian species of *Caldcluvia—C. australiensis* (FIGURE 61), *C. paniculosa* (FIGURE 67), and *C. rosifolia* (FIGURE 62). Three principal patterns of hair distribution are present: scattered, sparsely distributed, not confined to the ends of seeds (FIGURES 61, 62, 67, 87, 91, 102, 105, 112); in tuft restricted to the ends of seeds (FIGURES 83, 85, 88, 97, 100, 103, 106, 109); and abundant over the entire seed surface (FIGURES 92, 96). Intermediate conditions exist in which seeds are predominantly apically comate, with hairs also occasionally present on the sides (FIGURE 108). Great variation also occurs in hair length and abundance, with seeds ranging from sparsely

hirsute in *W. tinctoria* (FIGURE 91), *W. trichosperma* (FIGURE 112), and *W. bangii,* to very tomentose in such species as *W. pullei* (FIGURE 92) and *W. rubrinervis* (FIGURE 96). In *W. richii* tufts of long hairs are present at both ends of the seed, and short, almost papillalike hairs are scattered over the sides (FIGURES 94, 95). Seed hairs are simple, unicellular, sometimes striate, thin-walled structures without specialized ends such as hooks or barbs and are typically curved and intertwined in the mature seed.

Surface features of seeds belonging to this group of genera are likewise quite variable. Species differ not only in the more readily visible aspects of epidermal cell shape, size, outline, and wall characteristics, but also in the less conspicuous secondary features of external wall ornamentation. External epidermal cell walls are smooth, striate, warty, or a combination of striate and warty. Narrow cuticular striations mostly parallel with the long axes of epidermal cells have been observed in *Acsmithia elliptica, Acrophyllum australe* (FIGURE 80), *Caldcluvia celebica* (FIGURE 60), *Callicoma serratifolia* (FIGURE 78), and many species of *Weinmannia* such as *W. decora, W. dichotoma, W. pullei, W. tannaensis, W. trichosperma, W. richii,* and *W. purpurea* (FIGURES 84, 93, 113, 120). More or less irregularly oriented striations occur in *Cunonia macrophylla, Geissois biagiana, Caldcluvia fulva,* and *C. papuana* (FIGURES 43, 48, 70, 72). Striations vary considerably in size and abundance (compare FIGURES 111 and 113). A warty external surface has been noted in *Cunonia purpurea, Vesselowskya rubifolia, Weinmannia blumei, W. pinnata, W. subsessiliflora, W. negrosensis, W. hutchinsonii, W. descombesiana,* and *W. celebica* (FIGURES 45, 82, 104, 116, 117). Some species such as *W. affinis, W. monticola, W. serrata, W. sylvicola, W. luzoniensis, W. fraxinea, W. vescoi,* and *W. denhamii* (FIGURES 89, 98, 99, 101, 111, 114, 119) have both warts and striae. Warts vary in size and prominence and range in outline from circular (most commonly) to angular to sometimes rectangular (in *W. luzoniensis,* FIGURE 101).

A markedly papillate (tuberculate) condition, due to the unicellular protrusions of epidermal cells, distinguishes *Acrophyllum australe* (FIGURE 79) and *Callicoma serratifolia* (FIGURE 76), as well as *Caldcluvia brassii, C. paniculata* (FIGURE 64), *C. papuana* (FIGURE 69), *C. nymanii* (FIGURES 73, 74, 135), *C. clemensiae* (FIGURE 66), and *C. celebica* (FIGURES 58–60). Hoogland (1979) has drawn attention to the fact that among species of *Caldcluvia,* only the mature seed wall is papillate. Seeds of *Acrophyllum* are unique in being completely covered by papillae (FIGURE 79). Each papilla is generally broad and flattened at the base, smooth at the apex, and with a striate cuticle on the sides (FIGURE 80). Although the papillae of *Caldcluvia* are morphologically similar, they are scattered and cover the seed coat incompletely (FIGURES 59, 64, 66). As in *Acrophyllum,* the papillae are flattened at the base, rounded apically, and striate, differing only in that the striae extend over the apex (FIGURE 60). *Callicoma serratifolia* also produces papillate or tuberculate seeds with striate papillae (FIGURE 78). This observation is in agreement with that of Kennedy and Prakash (1981).

Scanning electron micrographs show that species of *Pancheria* have a distinctive seed surface in which enlarged epidermal cells of various outlines, with smooth, rounded outer walls, are arranged in mosaic patterns. These prominent

epidermal cells may completely cover the surface of both the wing and the seed body, as in *P. elegans* (FIGURES 35, 36), or they may be scattered over the seed surface along with less prominent cells of irregular outline, as in *P. sebertii* (FIGURE 34). Similar enlarged cells occur in *Cunonia schinziana* (FIGURE 50) and *C. macrophylla* (FIGURE 47). The surface of *C. purpurea* seeds, however, is composed of irregularly polygonal cells with thin, slightly raised lateral walls. Cells of irregular outline with moderately thick to thin lateral walls comprise the seed coats of *Lamanonia* (FIGURES 39, 40) and *Geissois stipularis* (FIGURES 37, 38). The Australian species of *Geissois* have diagnostic surface patterns: the epidermal cells of *G. benthamiana* seeds have raised outer walls covered with an unorganized arrangement of pits and irregular ridges and grooves (FIGURES 41, 42), while those of *G. biagiana* seeds have dome-shaped outer walls covered with prominent striations that are oriented at a flat to steep angle in relation to the inner walls (FIGURE 43). Narrowly rectangular surface cells with moderately thick and slightly raised lateral walls extending parallel with the long axis of the seed are present in *Vesselowskya rubifolia* (FIGURE 82). Structurally complex epidermal cells distinguish seeds of *Callicoma serratifolia.* These cells are thick walled and have a combination of thick surface ridges and striae forming intricate patterns of the type seen in FIGURE 77.

The seed-coat surface of *Spiraeanthemum katakata* and *S. samoense* generally has smooth, thin-walled, rectangular cells that tend to be without conspicuously raised anticlinal walls and are oriented with their long axes parallel to the long axis of the seed (FIGURE 53). *Acsmithia elliptica, A. densiflora, A. integrifolia,* and *A. pulleana* have a microreticulate sculpturing of small, square or rectangular to elongate cells with moderately thick, raised lateral walls (FIGURES 54, 56). It is particularly interesting that in some collections of *Acsmithia,* the surface pattern on the seed body is structurally different from that on the wings. In the taxa examined, surface cells on the wings are irregularly oriented, often interwoven, and fibrous looking—distinctly different in appearance from those on the body (FIGURES 54, 55). This feature has not been observed in other cunoniaceous genera.

The genus *Caldcluvia* includes plants with diverse surface features. In addition to the papillate condition described previously, the winged seeds of such species as *C. brassii* and *C. paniculata* have irregularly rectangular, hexagonal, or polygonal epidermal cells. Among the New Guinean species, *C. nymanii* appears distinctive in lacking obvious surface striations (FIGURE 75). *Caldcluvia australiensis, C. rosifolia,* and *C. paniculosa*—species with hairy seeds—have surface cells with raised and irregularly undulate anticlinal walls (FIGURES 62, 63, 68, 69).

Seed-surface patterns in *Weinmannia* are the most diverse in the family. In addition to the diversity discussed earlier, presence and distribution of striations and warts, and epidermal cell shape and wall characteristics are also quite variable. A reticulate surface composed of irregularly polygonal cells with moderately thick and raised radial walls occurs in *W. pinnata* (FIGURE 90) and *W. subsessiliflora* (FIGURE 87). A more irregular pattern of rectangular cells, in places approaching a rugulate condition, occurs in *W. decora* (FIGURE 120) and *W. tinctoria* (FIGURE 91). Vertically elongate cells of somewhat irregular outline

are present in a number of species. Variations in the appearance of this condition are illustrated in FIGURES 86, 107, and 118. In FIGURE 86 fine bars can be seen connecting the parallel ridges. A series of low, rounded ridges interspersed with small, spherical or polygonal warts is characteristic of *W. monticola* (FIGURE 89). The seed-coat surface of *W. tannaensis* consists of a series of undulating, usually longitudinally extended, low ridges and valleys (FIGURE 84); two ridges lying in close proximity are often connected by strands of wall material. The most common surface pattern in *Weinmannia* seeds is one of vertically elongated epidermal cells with raised, undulate anticlinal walls (FIGURES 95, 97, 102, 106, 107, 114–117). Low, irregularly undulating ridges are present in *W. luzoniensis, W. fraxinea,* and *W. denhamii* (FIGURES 101, 110, 111, 119). These ridges vary in height and width.

Histologically, the mature seed coat in these genera is composed of a cuticle and (four or) five (or more) layers of cells (FIGURES 23–26, 28). Four layers distinguish both *Acrophyllum australe* (FIGURE 30) and *Callicoma serratifolia,* whereas between six and eight cell layers characterize *Geissois.* This results in a three-layered testa and a one-, two-, or many-layered tegmen. Epidermal cells are cutinized, thin- or moderately thick-walled, and rectangular in transection. Surface cells in *Geissois* and *Pancheria* are typically enlarged and are often radially elongated as viewed in transection, with curved or dome-shaped outer walls (FIGURES 41, 42). In fully mature seeds of *Geissois,* the enlarged epidermal cells covering the wings may become very thick walled and sclerotic. Similarly enlarged cells also occur on the surface of some *Cunonia* seeds. The subepidermal layer is composed of rectangular or compressed, thin-walled, nonlignified cells. Among species examined, *Acrophyllum australe, Caldcluvia rosifolia, Cunonia pulchella, Geissois stipularis, Pancheria confusa, P. gatopensis,* and *Vesselowskya rubifolia* have a crystalliferous hypodermis (FIGURES 25, 28). Each crystal cell contains a solitary, angular crystal, although infrequent druses were observed in *G. stipularis.* Beneath the hypodermis a single layer of thick-walled, lignified, sclerotic cells is present in all taxa. These cells compose the only mechanical layer of the seed coat and are oriented longitudinally. Some variation exists among genera with regard to the shape and type of wall thickening of the sclerenchymatous cells as viewed in transection. While sclerenchyma cells are most commonly cuboidal or shortly radially elongate, with moderately thick walls, those of *Vesselowskya rubifolia* are small in diameter and have very thick walls (FIGURE 28). Seeds of *Acsmithia densiflora* (FIGURES 23, 136), *Caldcluvia rosifolia,* and *Weinmannia racemosa* have a sclerotic layer composed of cells with thickened inner and radial walls (U-shaped thickenings). Cells that are circular in transectional outline and have very thick walls occur in *Acrophyllum australe* (FIGURE 30). The tegmen consists of thin-walled, rectangular or compressed (crushed) cells, with the innermost layer always filled with a darkly staining substance.

INDEHISCENT-FRUITED GENERA

Nine genera are characterized by indehiscent fruits: *Aistopetalum* Schltr. (2 species), *Anodopetalum* A. Cunn. ex Endl. (1), *Ceratopetalum* J. E. Sm. (6),

Codia J. R. Forster & J. G. A. Forster (ca. 10), *Gillbeea* F. Mueller (2), *Platylophus* D. Don (1), *Pseudoweinmannia* Engler (2), *Pullea* Schltr. (3), and *Schizomeria* D. Don (ca. 18).

The fruits of these genera range from indehiscent capsules, drupes, and berries to the winged fruits of *Gillbeea* (FIGURES 8–14). Seed structure is also quite variable. I have found it most convenient, therefore, to describe each genus or group of genera individually.

The most common fruit type is an indehiscent, unilocular or bilocular capsule, characteristic of *Ceratopetalum, Codia, Pseudoweinmannia,* and *Pullea.* Fruits of *Ceratopetalum, Codia,* and *Pullea* may be derived from gynoecia with inferior or half-inferior ovaries, resulting in a fruit wall that is partially of hypanthial origin. Fruits of *Ceratopetalum* are bilocular, one- or two-seeded, and surrounded by enlarged, stellately spreading sepals (FIGURE 11). Up to four seeds occur in *Codia* and *Pseudoweinmannia* fruits, but only a single fertile one may be present in those of *Pullea glabra* var. *glabra.* Mature fruit walls range from glabrous to densely tomentose, as in *Codia* (FIGURE 14) and *Pseudoweinmannia,* respectively (FIGURES 12, 13).

Pericarps of *Ceratopetalum* and *Pullea* are differentiated into outer exocarp, middle mesocarp, and inner fibrous endocarp. Internal to the epidermis is a chiefly parenchymatous middle region that, in both genera, contains scattered brachysclereids. The sclereids in *P. glabra* are thin walled, whereas those in *C. succirubrum* are conspicuously thick walled and pitted. Enlarged "mucilage" cells are also present in *Pullea.* The generally narrow, fibrous, lignified endocarp is composed of thick-walled elements arranged in two zones, one oriented vertically and the other horizontally. Immediately external to the inner sclerenchymatous region in fruits of *Ceratopetalum* is a uniseriate prismatic layer in which each cell contains a solitary angular crystal.

The pericarp of *Pseudoweinmannia* also contains a prominent crystalliferous layer outside the lignified, multiseriate inner zone composed mostly of tangentially elongated fibrous cells. Mature fruits of *Pseudoweinmannia* develop characteristic placental proliferations that, at maturity, may largely fill the locules between seeds (FIGURE 21). Proliferations appear to be derived from the inner pericarp wall as well as from the placentae and have a folded appearance in sectional view; the seeds are situated between the folds. The placentae are composed of thin-walled parenchyma cells, although the lateral peripheral regions consist of two or three layers of moderately thick-walled elements that resemble endocarp tissue. The outer surface of the placenta is composed of one or two layers of conspicuously enlarged, elongated cells that are oriented radially.

The capsule wall of *Codia nitida* is composed of an outer layer of small, irregularly shaped epidermal cells and one to three layers of larger, moderately thick-walled hypodermal cells. Internal to the hypodermis is an interrupted ring of very thick-walled fibrous cells, some of which may surround the fruit vasculature. The inner half of the pericarp is constructed of loosely arranged aerenchyma, but a distinct sclerenchymatous endocarp is absent (FIGURES 144, 145).

Seeds of *Codia* and *Pullea* tend to be rather small (less than 1 mm long) and

are more or less narrowly ellipsoid to ellipsoid (FIGURES 121, 123, 124). *Pseudoweinmannia* produces slightly larger, spheroidal seeds with a somewhat lobed appearance (FIGURE 125). Seeds of *Codia* and *Pullea* are essentially without wings, although rudimentary terminal wings can be recognized in some specimens. Arillike appendages characterize seeds of *Pseudoweinmannia lachnocarpa*. These appear as a ring of rather small, distinct, localized outgrowths from the exostomal region of the testa (FIGURE 126). In the absence of developmental observations, the origin and function of these structures is uncertain, although the overall structure has the general appearance of an elaiosome.

The surface of *Pseudoweinmannia* seeds is smooth, composed of nonornamented epidermal cells with a polygonal outline (FIGURE 125). Seeds of *Codia nitida, C. obcordata, Pullea glabra* var. *glabra,* and *P. stutzeri* have a reticulate external surface composed of cells with moderately raised anticlinal walls and a polygonal or, more commonly, reticulate outline (FIGURE 122). Fine striations can be observed on the surface of *C. nitida.*

Seed coats of *Codia* and *Pullea* are thin and undifferentiated. Pigmented outer and inner epidermal layers bound a central region of one or two layers of thin-walled cells. Mechanical cells are absent (FIGURE 29). Outer epidermal cells have irregular outlines and outer walls that are dome shaped in transection. Seeds of *Codia* are supplied by a tenuous, undivided vascular bundle extending to the chalazal region, while those of *Pullea glabra* have a single bundle that subdivides and terminates within the chalaza.

In contrast with the seed coats of the two previous genera, those of *Pseudoweinmannia lachnocarpa* are composed of multiple layers with a centrally positioned zone of mechanical cells. Very enlarged outer epidermal cells lack tannin and in the apical regions of the seed are often radially elongated to the surface; epidermal cells typically have thickened outer and radial walls. Beneath the epidermis are two layers of thin-walled cells of irregular size and shape. Internal to this hypodermis is a uniseriate zone of small, relatively thin-walled, mechanical cells. The multiple tegmen is composed of approximately seven or eight layers, including the inner, tanniferous epidermis. Seeds are vascularized by a single bundle that terminates within the chalazal region and shows no evidence of branching.

Seed coats of *Ceratopetalum succirubrum* (FIGURE 27) develop a thick-walled outer layer of pigmented cells that are rectangular in transectional outline and covered by a cuticle. Beneath the epidermis are two or three layers of pigmented cells, including a layer containing large, scattered, prismatic crystals. The crystalliferous layer overlies a well-developed uniseriate region of sclerenchyma. The fibrous sclerenchymatous elements are of variable width and outline but are generally rather wide with very thick, lignified, pitted walls. The remaining tegmen contains five or six indistinct layers of compressed and pigmented cells. I was not able to interpret the pattern of seed vasculature from the material at hand.

The genus *Schizomeria* is characterized by ellipsoid to ovoid, one-locular, one-seeded, drupaceous fruits (FIGURES 8, 141). The pericarp is strongly differentiated into an outer exocarp, an extensive fleshy mesocarp, and an inner stony endocarp. The relatively thin exocarp is composed of a surface layer of

small, rectangular, thick-walled epidermal cells and a single hypodermal layer consisting of more or less rectangular thick-walled cells. The fleshy mesocarp contains very thin-walled parenchyma interspersed with numerous isolated brachysclereids and sclereid nests. Sclereids are thick-walled, highly pitted, and occasionally crystalliferous with a solitary druse in the cell lumen. The endocarp is constructed of interwoven, tangentially elongated fibrous elements. Numerous small prismatic crystals are present throughout the inner mesocarp and endocarp. Major vascular bundles are confined to the fleshy mesocarp.

The seed coat is tightly compressed against the inner pericarp wall, with the outer seed surface containing narrow grooves and ridges (FIGURE 129). Beneath a cuticular layer, the testal epidermis is composed of darkly staining cells that are mostly square in transection. Cells in the two subepidermal layers are rectangular and thin walled. Beneath the bilayered hypodermis is a distinctive uniseriate zone of columnar mechanical cells with unevenly thickened walls resembling hourglass cells (FIGURE 142). Immediately internal to the sclerenchymatous layer are one or two layers of small crystalliferous cells. These cells merge with the multiple-layered tegmen mesophyll that is derived by periclinal division in the fertilized ovule and is composed of at least 20 layers of enlarged, very thin-walled cells. Inner epidermal cells are rectangular in outline and very tanniferous (FIGURE 141). A single large raphe bundle subdivides near the chalazal end of the seed into a system of veins that terminates at the chalaza.

Fruits of *Aistopetalum* are four- to six-loculate, ovoid drupes. Each locule potentially contains a single oblong, pendulous seed (FIGURES 137, 138). Mature fruits of *A. viticoides* Schltr. average 20 mm in length and 13 mm in diameter, with seeds about 6 mm long (Hoogland, 1960).

Two immature fruits of *Aistopetalum multiflorum* were sectioned; these were 6 mm in diameter and 8 mm in length. The immature pericarp of the fruits is differentiated into exocarp, mesocarp, and endocarp on the basis of cell shape and differential retention of stain. The epidermis of the uneven outer surface of the pericarp, composed of small, rather irregularly shaped cells, is covered by a thin layer of cuticle. The hypodermis consists of five to seven layers of small cells with slightly thickened walls. The major portion of the pericarp contains isodiametric parenchyma cells of various sizes. Cells of the inner mesocarp are densely tanniferous. While immature, the endocarp is distinguished by highly tanniferous tissue (FIGURE 139). As the fruit matures, seven to ten layers of tangentially elongated elements adjacent to the locules become relatively thick walled and differentiate into a very hard endocarp. Crystals are absent from the pericarp in my material.

The immature seed coat is tightly compressed against the endocarp wall. The outer epidermis is densely pigmented and is composed of cells that are more or less square or rectangular in transectional outline. The remaining testa is generally made up of six to eight layers of tanniferous, isodiametric, thin-walled cells. A uniseriate layer composed of cells having very narrow diameters, angular outlines, and moderately thick walls separates testa and tegmen. The multiple-layered tegmen consists of six to eight layers of large, thin-walled cells that are often radially aligned, as well as an inner, tanniferous epidermis. Crystals are absent from the seed coat. A single vascular bundle enters the seed,

extends through the parenchymatous testa (FIGURE 139), and branches freely within the chalazal region to form numerous veins that become arranged within the chalazal end of the seed (FIGURE 140).

The third genus with fleshy fruits is *Anodopetalum*. The pericarp of *Anodopetalum*, in contrast with those of *Schizomeria* and *Aistopetalum*, is unlignified and not strongly differentiated. The fruit is therefore a berry. An outer exocarp is characterized by a layer of small, rectangular epidermal cells and up to six subepidermal layers of collenchyma. An extensive mesocarp contains parenchymatous cells and numerous scattered, highly pitted, relatively thin-walled brachysclereids. Vasculature is confined to the middle zone and, as in other fleshy fruit types of the Cunoniaceae, is not associated with ensheathing sclerenchyma. The inner pericarp region lacks sclerenchyma but is recognizable by a ring of crystalliferous cells containing acicular, clustered crystals that are accompanied by small, irregular, angular forms (FIGURE 143). The acicular crystals are more or less needlelike but have blunt ends, so they are somewhat intermediate between raphides and styloids.

In my reexpanded material the seed coat is not well preserved, but it can be determined to be parenchymatous and to consist of more than ten cell layers. Epidermal cells are irregular in outline and often have dome-shaped outer walls. A distinct layer of sclerenchyma is absent. As in the other cunoniaceous genera with fleshy fruit, seeds are vascularized by a single vein that divides repeatedly in the lower half of the seed before ending within the chalaza.

The indehiscent trilocular fruit of *Gillbeea* has three prominent wings that extend the length of the central fruit column and are formed by the lateral expansion of the carpel wall (FIGURES 10, 15). Hoogland (1960) described the carpels as each containing a single seed, although only one fertile locule existed in each of the two fruits sectioned for this study (FIGURE 15).

The wings have a prominent reticulate venation, which in mature fruits is surrounded by massive sclerenchymatous sheathing. The pericarp is composed of small epidermal cells, a parenchymatous mesocarp, and a narrow, two- or three-layered endocarp composed of fibrous elements, which is separated from the parenchymatous outer region by a crystalliferous layer containing angular crystals.

Seeds of *Gillbeea* are oblong and about 5–8 mm long. The seed coat in the material examined is rather homogeneous in construction, with three or four layers of relatively thick-walled, pigmented, greatly compressed cells. I have not been able to detect a sclerenchymatous layer. The testal epidermis is conspicuously papillate or tuberculate (FIGURE 16). As in other Cunoniaceae, the projections represent unicellular extensions of epidermal cells (FIGURE 17). As observed from sectioned specimens, the tuberculae are broad at the base, with rounded apices and with surface striae extending parallel to the long axis of the projection. Presumably, some of the projections are glandular and secrete the dark, resinous substances that cover the seeds of species of this genus. I have not been able to detect whether the single vascular bundle present at midlength in the seed undergoes subsequent branching.

The fruit of the monotypic South African genus *Platylophus* is derived from a bicarpellate gynoecium and, at maturity, is bilocular but most commonly

one seeded. Its basal region is turgid, and the apical half is distinctly compressed (FIGURE 9). The fruit has been described as an imperfectly dehiscent capsule (Harvey, 1894) that remains closed for an extended period. I have seen no dehisced fruits.

In *Platylophus* the pericarp is covered by epidermal cells with decidedly thickened and pitted outer and anticlinal walls. A narrow mesocarp is constructed of very thin-walled parenchyma cells, although its veins are surrounded by sclerenchymatous sheathing. A thin, two- or three-layered, fibrous, lignified endocarp is separated from the outer mesocarp by a region containing angular crystals (FIGURE 18).

Seeds are elliptic, less than 1 mm in length, and sometimes with vestigial wings (FIGURE 127). The seed surface is finely reticulate, with the individual cells generally square or rectangular in outline and having slightly raised lateral walls (FIGURE 128). The minute, spherical warts that cover the external cell walls in FIGURE 128 are apparently artifacts, since they were not present in all specimens examined.

The narrow seed coat is relatively undifferentiated and lacks a distinct sclerenchyma layer. Internal to the pigmented outer epidermis is a hypodermis containing scattered angular crystals and two layers of compressed cells that are rectangular in transectional outline. The internal epidermis is similar to the outer one, except that the cells are smaller.

DISCUSSION

GENERAL SUMMARY OF FRUIT AND SEED STRUCTURE

Plants belonging to the Cunoniaceae are readily divisible into genera with dehiscent fruits (either follicles or bilocular capsules) and indehiscent ones (dry—capsular or winged; or fleshy—drupes or berries). Fruit wings of *Ceratopetalum* are derived from an expanded and hardened calyx, whereas the winglike outgrowths of *Gillbeea* fruits represent extensions of the gynoecial wall. Dehiscent capsules open septicidally from the apex downward or, less commonly, from the base upward. Fruits of *Ceratopetalum, Codia,* and *Pullea* are typically derived from inferior or half-inferior ovaries. Fruit walls range from glabrous to densely pubescent.

Most species of Cunoniaceae produce fruits in which the pericarp becomes differentiated into an exocarp, a mesocarp, and a lignified, fibrous endocarp. The endocarp portion ranges in thickness from about 50 μm in fruits of some species of *Weinmannia* to just over 600 μm in plants of *Geissois,* with a distinct woody endocarp entirely absent only in *Codia* and the fleshy-fruited genus *Anodopetalum*. *Codia* is unique in having aerenchymatous inner pericarp tissue (FIGURES 144, 145). The drupaceous fruits of *Aistopetalum* and (particularly) *Schizomeria* contain an extensive fleshy mesocarp. Fruit walls range in thickness from rather thin (four to eight cells) to very thick (forty cells); they typically contain scattered prismatic or druse crystals, or crystals (rarely acicular ones—*Anodopetalum*) restricted to the inner mesocarp and endocarp. In certain species of *Anodopetalum, Ceratopetalum, Cunonia, Pullea,* and *Schizomeria,* brachysclereids are distributed throughout all three regions of the pericarp.

Dehiscent-fruited genera form one to numerous viable seeds per locule, ranging in length from small (0.4 mm) to rather large (6 mm), with the ovular integuments uniformly developing wings or hairs at maturity. Seeds are generally apically comate, although less commonly hairs are distributed in other patterns. The only exception to the above generalization is the monotypic Australian genus *Acrophyllum*, which forms small, conspicuously papillate (tuberculate) seeds. External seed surfaces are quite diverse in ornamentation. Variable features include shape and wall characteristics of the epidermal cells, and occurrence, type, and abundance of striations and warts.

Seed coats are derived from both ovular integuments and are thin—one to five cells thick, except in *Geissois*, where they may be up to seven cells in thickness. Testae are relatively undifferentiated and generally contain an outer and an inner tanniferous layer. All taxa have a single fibrous layer that, as far as can be determined, is always derived from the outer epidermis of the inner integument. A distinct crystalliferous layer is present in the hypodermis in certain species.

Genera with indehiscent fruits produce one to several seeds per fruit and a variety of seed morphologies. Seeds range in size from small (less than 1 mm in length) in *Codia* and *Pullea* to rather large (up to 5–6 mm in length) in *Aistopetalum* and *Schizomeria*. Although seeds of all genera are devoid of external wall appendages in the form of wings or hairs, those of *Pseudoweinmannia* are unique among the Cunoniaceae in having an arillike outgrowth with the general appearance of an elaiosome. Seed surfaces are smooth (*Pseudoweinmannia*), reticulate (*Codia, Pullea*), or papillate (*Gillbeea*).

Mature seed coats are thin (three or four cells), and either undifferentiated and lacking a mechanical zone (*Codia, Pullea*) or multiple layered and with a well-differentiated fibrous layer (*Schizomeria, Pseudoweinmannia*). Multiple-layered seed coats arise by secondary division within the integumentary layers of fertilized ovules. In *Anodopetalum* multiple seed-coat layers appear to be associated with the absence of a mechanical zone, but this observation requires additional documentation. As in seeds from dehiscent-fruited taxa, one or more crystalliferous layers may be present in certain species.

All cunoniaceous seeds are vascularized by a single bundle, which in some fleshy-fruited genera undergoes branching within the chalaza. All Cunoniaceae have straight embryos that at maturity are embedded in an abundant endosperm.

EVOLUTIONARY TRENDS IN FRUIT STRUCTURE AND IN SEED STRUCTURE AND DISPERSAL

The diversity encountered among fruits and seeds of the Cunoniaceae clearly represents a range of different levels of evolutionary advancement and dispersal methods. A major trend of specialization occurs toward the indehiscent condition. A summary of fruit types and methods of seed dispersal in the Cunoniaceae is presented in TABLE 2. Although the bilocular, ventrally dehiscent capsule is the most common fruit type in the family, all available evidence indicates that apocarpy—and the resultant follicular fruits, such as those found in *Acsmithia* and *Spiraeanthemum*—is the primitive condition in the family

TABLE 2. **Summary of fruit types and methods of seed dispersal in Cunoniaceae.**

GENUS	DISTRIBUTION	HABIT	FRUIT TYPE	AGENT OF DISPERSAL	ADAPTATION FOR DISPERSAL
DEHISCENT FRUITS					
Acrophyllum	New South Wales	Subshrubs	Capsule	?	Seeds papillate
Acsmithia	Fiji, New Caledonia, Queensland, New Guinea, Moluccas	Small to medium trees	Follicle	Wind	Seeds winged
Bauera	E Australia	Small shrubs, subshrubs	Capsule	?	?
Caldcluvia	Chile, New Zealand, Australia, Philippines, Celebes, Moluccas, New Guinea, Solomon Is. Bougainville Is.	Small to large trees	Capsule	Wind	Seeds winged, papillate, hairy
Callicoma	E Australia	Small trees, shrubs	Capsule	Wind	Seeds winged, papillate
Cunonia	New Caledonia, South Africa	Small to medium trees, shrubs	Capsule	Wind	Seeds winged
Geissois	Fiji, New Caledonia	Small to medium trees	Capsule	Wind	Seeds winged
Lamanonia	Brazil, Paraguay	Trees, shrubs	Capsule	Wind	Seeds winged
Pancheria	New Caledonia	Small trees, shrubs	Capsule	Wind	Seeds winged
Spiraeanthemum	Samoa, Fiji, New Hebrides, Solomon Is., New Britain, Bougainville Is.	Shrubs, small to medium trees	Follicle	Wind	Seeds winged
Vesselowskya	E Australia	Small trees, shrubs	Capsule	Wind	Seeds winged
Weinmannia	Old and New World tropics	Small to medium trees, shrubs	Capsule	Wind	Seeds hairy
INDEHISCENT FRUITS					
Aistopetalum	New Guinea	Tall trees	Drupe	Animals(?)	Fruits fleshy
Anodopetalum	Tasmania	Shrubs	Berry	Animals(?)	Fruits fleshy
Ceratopetalum	E Australia, New Guinea	Large shrubs, small to large trees	Capsule	Wind	Fruits winged
Codia	New Caledonia	Shrubs, small trees	Capsule	Wind	Fruits hairy
Gillbeea	Queensland, New Guinea	Medium to large trees	Winged	Wind	Fruits winged
Platylophus	South Africa	Medium to large trees	Capsule	Water	Fruits turgid
Pseudoweinmannia	Queensland, New South Wales	Large trees	Capsule	Wind (and ants?)	Fruits hairy, seeds with elaiosomes
Pullea	Fiji, Queensland, Moluccas, New Guinea	Small to medium trees	Capsule	?	?
Schizomeria	E Australia, New Guinea, Solomon Is.	Medium to large trees	Drupe	Animals(?)	Fruits fleshy

and is not derived as suggested by Cuatrecasas (1970). The initial evolutionary step, therefore, involved the conversion of a cluster of follicles into a septicidally dehiscent capsule.

In all the genera considered to be primitive on the basis of floral morphology and wood anatomy, the seed is thin walled, has a single, lignified, fibrous layer, and acts as the sole dispersal unit. With the notable exception of *Acrophyllum*, all dehiscent-fruited genera produce seeds with structural modifications—either membranous wings or hairs—for dispersal by wind. Appendages have apparently been lost from the seeds of *Acrophyllum*, although the surface cells have prominent papillae or tuberculate outgrowths. In contrast with other taxa, *Acrophyllum* is a small (usually under 1 m tall) shrub or subshrub that has a very restricted distribution in the Blue Mountains of New South Wales, where it grows only on moist ledges in the immediate vicinity of waterfalls.

Subsequent evolutionary advancement has resulted in major shifts in dispersal methods. In the more advanced cunoniaceous taxa, the entire fruit has become modified for dispersal and protection, and there have been reductions in the number of seeds per fruit. Distinct trends of structural specialization in the fruit have resulted in densely pubescent (*Codia, Pseudoweinmannia*) and winged (*Ceratopetalum, Gillbeea*) fruit types that are associated with anemochory. Moreover, the two winged types of fruit represent different evolutionary trends since the wings are derived from different sources (in *Ceratopetalum* they derive from an enlarged and hardened calyx, whereas in *Gillbeea* they are gynoecial in origin). In *Anodopetalum, Codia*, and *Bauera* a lignified endocarp in the fruit wall has been lost (Prakash & McAlister, 1977). The adaptive significance of pericarp aerenchyma in *Codia* is unclear. *Pseudoweinmannia*, a tall rainforest tree from Queensland and New South Wales, is interesting in that its densely hairy, indehiscent fruits are undoubtedly scattered by wind, but its elaiosomelike seed appendages suggest that a secondary agent (perhaps an ant) may also be involved in dispersal.

Trends have also occurred toward formation of drupaceous and berrylike fruits. Although method(s) of dispersal for these fruit types is unknown for the Cunoniaceae, such adaptations generally promote seed dispersal by animals. For *Platylophus*, which usually grows near streams and rivers, Ridley (1930) repeated earlier observations that the fruits are dispersed by flowing water. Ben-Erik van Wyk, of the University of Stellenbosch, has observed (pers. comm.) that the turgid capsules break off, leaving the entire pedicel on the inflorescence, and that capsules are frequently seen floating on water. The inflated fruit wall and the absence of dispersal structures on the small, thin-walled seeds may be reflections of this adaptation. Within the family there have thus been major adaptive shifts in dispersal agents—from wind to animal, and even water.

Seeds have undergone concomitant changes. Accompanying the general loss of dispersal appendages, at least two distinct trends are evident in seed-coat structure: reduction in seed-coat thickness, including the loss of a mechanical layer (e.g., *Codia, Platylophus, Pullea*); and amplification of the seed coat by secondary division of integumentary cells in the fertilized ovule to form a

multiple-layered seed coat (e.g., *Aistopetalum, Schizomeria*). A secondary increase in seed-coat layers may or may not be accompanied by loss of a fibrous layer. I cannot accept Krach's (1977) suggestion that all seed coats in the Cunoniaceae were derived via a general trend toward reduction from a multilayered ancestral condition. The various genera of Cunoniaceae are, therefore, good examples of what Corner (1958) and later Stebbins (1970, 1974) referred to as the "transference of function" with respect to the protection and dispersal of seeds. I am uncertain of the significance of the resinous coating on seeds of *Gillbeea*.

It is of interest to note the general correlation between the production of indehiscent fruits with more specialized seed types and a more advanced wood anatomy. The genera *Aistopetalum, Anodopetalum, Bauera, Ceratopetalum, Codia, Pseudoweinmannia,* and *Schizomeria* all have vessel elements with exclusively or predominantly simple perforation plates (Dickison, 1980b). The only exceptions to this correlation are *Gillbeea* and *Pullea,* which have vessel elements with scalariform perforations.

Fruit and Seed Morphology and Intrafamilial Systematics

I have previously pointed out (Dickison, 1980b) that evidence is accumulating to indicate that many of the tribes of Cunoniaceae, as defined by Engler (1928), are very unnatural assemblages that should be either reconstructed or abandoned. The morphology of fruits and seeds supports this opinion. Although the family can be divided into groups and subgroups, representing different levels of specialization, by the use of various characters, it is clear that fruit morphology should be important in any future subdivision of the family.

Engler's tribe Belangereae, containing the southwestern Pacific genus *Geissois* and the Neotropical *Lamanonia,* is from all indications a natural grouping. The two genera both lack petals and have numerous stamens and a bicarpellate superior gynoecium that matures into a septicidally dehiscent capsule containing comparatively large winged seeds. Both also have a structurally advanced wood anatomy (Dickison, 1980b) that is correlated with other indices of advancement such as fourth-rank leaves (*sensu* Hickey, 1971) and, at least in *Geissois,* multilacunar nodal anatomy (Dickison, 1980a).

I emphasized in an earlier paper (Dickison, 1980b) that the tribe Spiraeanthemeae is a very heterogeneous aggregation that includes the primitive genus *Spiraeanthemum* (including the segregate genus *Acsmithia*), with primitive wood anatomy, as well as the rather advanced genus *Aistopetalum.* Extreme diversity is also apparent in reproductive morphology. *Spiraeanthemum* (and *Acsmithia*) have follicular fruits with winged seeds, whereas the drupaceous fruit of *Aistopetalum* and the winged fruit of *Gillbeea* are both significantly more advanced and represent quite different dispersal methods. Although all species in this tribe have flowers with a mostly three- to five-carpellate gynoecium and a stamen number equal to or double the number of sepals, they differ with respect to such other characters as sepal aestivation (imbricate or valvate)

and gynoecium type (apocarpous to syncarpous). The genus *Aphanopetalum* appears to be best removed from the family for reasons previously outlined (Dickison, 1980b).

Engler defined his Cunonieae, the largest tribe of Cunoniaceae, by the following characters: stamens equal to or double the number of sepals; gynoecium superior, bicarpellate, with the carpels more or less fused ventrally in the region of the ovary; petals present or absent; sepals imbricate or valvate; and flowers not produced in a dense spherical head.

On the basis of vegetative anatomy, this is the most diverse group, with genera representing quite different levels of evolutionary advancement (Dickison, 1980b). This is also true for the fruits and seeds of the tribe, which represent major differences in dispersal methods. Both dehiscent and indehiscent fruits are present. The most frequent type is the dehiscent capsule, such as occurs in *Acrophyllum, Caldcluvia, Cunonia, Vesselowskya,* and *Weinmannia.* There are also more advanced, indehiscent capsules (*Ceratopetalum, Pseudoweinmannia*), drupes (*Schizomeria*), and berries (*Anodopetalum*).

Hoogland (1979) has reduced the Australasian genera *Ackama* A. Cunn., *Betchea* Schltr. (including *Stollaea* Schltr.), *Opocunonia* Schltr., and *Spiraeopsis* Miq. to synonymy with the monotypic Chilean genus *Caldcluvia.* The diversity in wood structure among these taxa has already been discussed (Dickison, 1980b). Hoogland (1979) noted that the flowers and fruits of these species are too much alike to merit recognition as separate genera. The seeds, however, are different, as was pointed out by Hoogland. The three Australian and New Zealand species formerly included in *Ackama* all have hairy seeds and similar surface patterns, with epidermal cells having conspicuously undulate anticlinal walls. All other taxa in this complex have winged, frequently papillate seeds with striate or nonstriate (*C. nymanii*) epidermal cells.

Hoogland (1979) further stated that *Caldcluvia* is similar to *Weinmannia* in flower and fruit, being most easily separated on the basis of inflorescence structure. In addition, relationship between *Caldcluvia* and *Weinmannia* is indicated by the occurrence of apically comate seeds in species of both genera. It should also be reemphasized that the only apparent characters that would argue against a merger of *Weinmannia* and *Cunonia* are those associated with fruit dehiscence and seed morphology. Seeds of *Weinmannia* are always hirsute, whereas those of *Cunonia* are uniformly winged. Since both character states currently exist in *Caldcluvia,* however, the strength of this distinction is weakened.

In Engler's scheme the tribe Pancherieae, which contains the three genera *Callicoma, Codia,* and *Pancheria,* is held together by flowers that are characteristically produced in tightly compacted, globose clusters. Xylem anatomy is quite variable among these genera, which also show both imbricate and valvate sepal aestivation, superior and inferior gynoecia, and dehiscent (*Callicoma, Pancheria*) and indehiscent (*Codia*) fruits producing seeds of quite different structure. The fruits of *Codia,* in contrast to those of *Callicoma* and *Pancheria,* lack a lignified endocarp, and its seeds also lack a mechanical layer. I think that a similar inflorescence type has evolved among diverse elements.

The last tribe, Pulleae, contains the single genus *Pullea,* characterized by a

rather primitive wood structure, apetalous flowers, imbricate sepals, and a bicarpellate, "half-inferior" ovary that matures into an indehiscent capsule. Seeds of *Pullea, Codia,* and *Platylophus* are similar in size, in lack of a fibrous layer in the seed coat, and in surface patterns.

The systematic position of the Australian and Tasmanian genus *Bauera* Banks has been somewhat unsettled (Dickison, 1975c). Despite my earlier opinion to the contrary (Dickison, 1975c), recent evidence strongly favors a position in the Cunoniaceae (Bensel & Palser, 1975; Prakash & McAlister, 1977). Aspects of vegetative anatomy would place the genus among the more advanced genera within the family (Dickison, 1980b). The fruits of *Bauera* are dehiscent capsules with seeds that develop a multiple-layered tegmen and apparently lack a mechanical layer (Prakash & McAlister, 1977). This is an uncommon combination of features in the Cunoniaceae, occurring elsewhere only in *Anodopetalum.* A secondary increase in seed-coat layers and an absence of a thick-walled lignified cell layer are both, in my opinion, advanced characteristics among cunoniaceous seeds.

The use of scanning electron microscopy has revealed considerable variation in shape, pattern of hair distribution, and surface characteristics of the seeds. This is particularly true in the large and widely distributed genus *Weinmannia.* Although in a few cases features appear to be diagnostic for species, a much greater sample would need to be examined to assess fully the taxonomic usefulness of seed morphology at the subgeneric and specific levels.

Comments on the Relationships of Cunoniaceae to Other Families

As reviewed by Dickison (1975a, 1980b), the Cunoniaceae have traditionally been placed in a basal position within the large order Rosales, in or near the saxifragaceous complex (Engler, 1928; Schulze-Menz, 1964; Cronquist, 1981). Families that have long been closely allied with the Cunoniaceae include the Saxifragaceae, Eucryphiaceae, Brunelliaceae, and Staphyleaceae. Since the seed structures of this complex are incompletely known, it would be premature to attempt a discussion of relationships based upon this criterion. However, a few observations can be made.

The present study further substantiates the significant differences in seed-coat structure between the Cunoniaceae (including *Bauera*) and the Saxifragaceae that have been summarized by Prakash and McAlister (1977). Seed coats of the Cunoniaceae are uniformly derived from both integuments, whereas those of the Saxifragaceae apparently mature only from the outer integument, with the inner tegmen degenerating. Corner (1976) has indicated that there is a significant evolutionary distinction between families with exotestal seed construction (Saxifragaceae) and those with exotegmic seed construction (Cunoniaceae). The additional important distinctions (relating to aspects of embryology) between these families require documentation.

The small neotropical family Brunelliaceae, characterized by apocarpous, apetalous, diplostemonous flowers, in this respect resembles the cunoniaceous genera *Acsmithia* and *Spiraeanthemum.* Each carpel matures into a follicle in

which the pericarp becomes strongly differentiated into outer parenchymatous exocarp and inner woody endocarp (Eyde, 1970). The asymmetric growth of the ovary that displaces the style to the abaxial side—and the resulting specialized fruit—is constant in all members of the Brunelliaceae and is not matched in any possibly related family (Cuatrecasas, 1970). Seeds of *Brunellia* lack dispersal appendages, and the testa is thick. Wood anatomy of the genus is at a higher evolutionary level than that of the more primitive genera of Cunoniaceae (Dickison, 1980b).

Over the years various individuals (Hallier, 1908; Linden, 1960; Whitmore, 1972; Thorne, 1976) have strongly emphasized affinities between the Staphyleaceae and the Cunoniaceae. Similarity is evidenced in the fibrous exotegmic seeds of the staphyleaceous genera *Huertea* Ruiz & Pavon and *Tapiscia* D. Oliver (Corner, 1976) and the exotegmic seeds of the Cunoniaceae.

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EXPLANATION OF PLATES

PLATE I

FIGURES 1–14. Fruit morphology of Cunoniaceae. 1, *Spiraeanthemum macgillivrayi* (*Morrison 25.6.1896*), × 5.5. 2, *Weinmannia blumei* (*Dickison 215*), × 5. 3, *Cunonia macrophylla* (*Webster & Hildreth 14493*), × 1.5. 4, 5, *Pancheria sebertii* (*Franc 2109*): 4, mature fruit head, × 1.5; 5, individual fruit valve, × 3. 6, *Geissois stipularis* (*Fiji Herb. 31297*), × 1. 7, *Acrophyllum australe* (*Stauffer et al. 5700*), × 3. 8, *Schizomeria ilicina* (*Brass 12150*), × 1. 9, *Platylophus trifoliatus* (*Bolus 621*), × 3. 10, *Gillbeea papuana* (*Brass 31815*), × 1.5. 11, *Ceratopetalum succirubrum* (*Hartley 10967*), × 1.5. 12, 13, *Pseudoweinmannia lachnocarpa* (*Clemens 43294*), × 2.5: 12, mature fruit; 13, mature fruit with tomentum partially removed. 14, *Codia nitida* (*Dickison 221*), × 2.5.

PLATE II

FIGURES 15–22. Fruit anatomy of Cunoniaceae. 15–17, *Gillbeea papuana* (*Brass 31815*): 15, transverse section of mature fruit; 16, transverse section of mature seed; 17, seed epidermis showing papillae. 18, *Platylophus trifoliatus* (*Bolus 621*), transverse section of pericarp. 19, *Acsmithia densiflora* (*Dickison 220*), transverse section of follicle. 20, *Weinmannia racemosa* (cult., E), transverse section of capsule. 21, *Pseudoweinmannia lachnocarpa* (*Dickison & Jessup 294*), transverse section of fruit showing placental proliferations. 22, *Geissois stipularis* (*Fiji Herb. 31297*), transverse section of capsule (only major veins illustrated).

PLATE III

FIGURES 23–30. Seed-coat structure in Cunoniaceae: 23, *Acsmithia densiflora* (*Dickison 220*); 24, *Caldcluvia nymanii* (*Hoogland & Craven 11069*); 25, *Cunonia pulchella* (*Dickison 218*); 26, *Pancheria hirsuta* (*Dickison 227*); 27, *Ceratopetalum succirubrum* (*Croft & Marsh, LAE 71177*); 28, *Vesselowskya rubifolia* (*Schodde 3210*); 29, *Codia nitida* (*Dickison 221*); 30, *Acrophyllum australe* (*Stauffer et al. 5700*) (CR, crystalliferous layer; CU, cuticle; EN, endosperm; EP, epidermis; IT, inner tegmen; S, sclerenchymatous layer; stippled cells pigmented).

PLATE IV

FIGURES 31–39. Scanning electron micrographs of seeds of Cunoniaceae. 31, 32, *Pancheria confusa* (*Veillon 66*): 31, side view, × 9; 32, hilar region, × 20. 33, 34, *P. sebertii* (*Franc 2109*): 33, side view, × 9; 34, surface, × 40. 35, 36, *P. elegans* (*Dickison 158*): 35, oblique side view, × 25; 36, surface, × 50. 37, 38, *Geissois stipularis* (*Fiji Herb. 31297*): 37, side view, × 8; 38, surface, × 22. 39, *Lamanonia ternata* (*Irwin et al. 8603*), side view, × 6.5.

PLATE V

FIGURES 40–48. Scanning electron micrographs of seeds of Cunoniaceae. 40, *Lamanonia tomentosa* (*Balansa 4752*), surface, × 50. 41, 42, *Geissois benthamiana* (*Forest Guard, Lismore 3.1909*), surface: 41, × 50; 42, × 500. 43, *G. biagiana* (*Dockrill 34*), surface, × 500. 44, 45, *Cunonia purpurea* (*Dickison 144*): 44, side view, × 15; 45, surface, × 150. 46–48, *C. macrophylla* (*Bernardi 9507*): 46, oblique side view, × 16; 47, surface, × 50; 48, surface, × 500.

PLATE VI

FIGURES 49–57. Scanning electron micrographs of seeds of Cunoniaceae. 49, 50, *Cunonia schinziana* (*McKee 23112*): 49, side view, × 14; 50, surface, × 40. 51, *C. pseudoverticillata* (*McKee 4410*), side view, × 20. 52, 53, *Spiraeanthemum katakata* (*Smith 4371*): 52, side view, × 15; 53, surface, × 200. 54, *Acsmithia elliptica* (*Veillon 2844*), side view, × 20. 55, 56, *A. densiflora* (*Musselman et al. 5222*): 55, side view, × 21; 56, surface, × 200. 57, *A. reticulata* (*Galore & Wood, NGF 41005*), side view, × 20.

PLATE VII

FIGURES 58–66. Scanning electron micrographs of seeds of Cunoniaceae, *Caldcluvia*. 58–60, *C. celebica* (*Havel & Kairo, NGF 17084*): 58, side view, × 30; 59, surface, × 100; 60, papillae, × 300. 61, *C. australiensis* (*Hoogland 8538*), side view, × 20. 62, 63, *C. rosifolia* (*Walker s.n.*): 62, side view, × 50; 63, surface, × 100. 64, *C. paniculata* (*Dombey 713*), surface, × 50. 65, *C. brassii* (*Brass 29616*), side view, × 23. 66, *C. clemensiae* (*Van Balgooy 969*), surface, × 50.

PLATE VIII

FIGURES 67–75. Scanning electron micrographs of seeds of Cunoniaceae, *Caldcluvia*. 67, 68, *C. paniculosa* (*Thorne et al. 25938*): 67, side view, × 20; 68, surface, × 200. 69, 70, *C. papuana* (*Kalkman 5316*): 69, side view, × 50; 70, surface, × 500. 71, 72, *C. fulva* (*Van Royen, NGF 18266*): 71, oblique side view, × 30; 72, surface, × 500. 73–75, *C. nymanii* (*Stevens, NGF 50443*): 73, side view, × 15; 74, surface, × 50; 75, surface, × 500.

PLATE IX

FIGURES 76–84. Scanning electron micrographs of seeds of Cunoniaceae. 76–78, *Callicoma serratifolia* (*White 10279*): 76, oblique side view, × 30; 77, surface, × 200; 78, detail of papillae, × 100. 79, 80, *Acrophyllum australe* (*Stauffer et al. 5700*): 79, side view, × 50; 80, detail of surface, × 500. 81, 82, *Vesselowskya rubifolia* (*White 11482*): 81, side view, × 15; 82, surface, × 150. 83, 84, *Weinmannia tannaensis* (*Bernardi 12909*): 83, side view, × 30; 84, surface, × 300.

PLATE X

FIGURES 85–93. Scanning electron micrographs of seeds of Cunoniaceae, *Weinmannia*. 85, 86, *W. racemosa* (*Philipson et al. 349*): 85, oblique side view, × 14; 86, surface, × 100. 87, *W. subsessiliflora* (*Vasquez A130*), side view, × 23. 88, 89, *W. monticola* (*McKee 23892*): 88, side view, × 40; 89, surface, × 400. 90, *W. pinnata* (*Sousa & Rico 8118*), side view, × 24. 91, *W. tinctoria* (*Bernardi 14516*), oblique side view (arrow points to hilum), × 20. 92, 93, *W. pullei* (*Hoogland & Schodde 7242*): 92, side view, × 16; 93, surface, × 350.

PLATE XI

FIGURES 94–102. Scanning electron micrographs of seeds of Cunoniaceae, *Weinmannia*. 94, 95, *W. richii* (*A. C. Smith 6813*): 94, side view, × 40; 95, surface, × 200. 96, *W. rubrinervis* (*D'Alleizette s.n.*), side view, × 20. 97, 98, *W. serrata* (*Bernardi 12816*): 97, side view, × 40; 98, surface, × 1000. 99, *W. sylvicola* (*Van Steenis 22314*), surface, × 500. 100, 101, *W. luzoniensis* (*Gacad, FB 27274*): 100, side view, × 40; 101, surface, × 500. 102, *W. glabra* (*Lansberger s.n.*), side view, × 50.

PLATE XII

FIGURES 103–111. Scanning electron micrographs of seeds of Cunoniaceae, *Weinmannia*. 103, 104, *W. negrosensis* (*Ramos, Philippine Plants 1287*): 103, oblique side view, × 20; 104, surface, × 1000. 105, *W. mauritiana* (*D'Alleizette 2166*), side view, × 40. 106, 107, *W. descombesiana* (*Eyma 3590*): 106, side view, × 40; 107, surface, × 200. 108, *W. trichophora* (*Pullen 374*), side view, × 20. 109–111, *W. fraxinea* (*Foreman 51*): 109, oblique side view, × 20; 110, surface, × 200; 111, surface, × 500.

PLATE XIII

FIGURES 112–120. Scanning electron micrographs of seeds of Cunoniaceae, *Weinmannia*. 112, 113, *W. trichosperma* (*Zollner 3137*): 112, side view, × 40; 113, surface, × 500. 114, *W. vescoi* (*Van Balgooy 1796*), surface, × 200. 115, 116, *W. celebica* (*Van Balgooy 3809*): 115, side view, × 40; 116, surface, × 200. 117, *W. hutchinsonii* (*Mendoza, PNH 18409*), surface, × 200. 118, *W. purpurea* (*Kajewski 1738*), surface, × 400. 119, *W. denhamii* (*Bernardi 13258*), surface, × 200. 120, *W. decora* (*Bernardi 11961*), surface, × 300.

PLATE XIV

FIGURES 121–129. Scanning electron micrographs of seeds of Cunoniaceae. 121, 122, *Codia nitida* (*Jaffre 2223*): 121, side view, × 60; 122, surface, × 200. 123, *Pullea stutzeri* (*Irvine 1253*), side view, × 100. 124, *P. glabra* (*Brass 31156*), side view, × 100. 125, 126, *Pseudoweinmannia lachnocarpa* (*Clemens 43294*): 125, side view (arrows point to arillike outgrowth), × 2; 126, detail of outgrowth, × 75. 127, 128, *Platylophus trifoliatus* (*Bolus 621*): 127, side view, × 50; 128, surface, × 500. 129, *Schizomeria whitei* (*Dickison 205*), surface, × 2000.

PLATE XV

FIGURES 130–136. Structure of fruits and seeds in Cunoniaceae, transverse sections. 130, 131, *Cunonia balansae* (*Dickison 230*): 130, immature fruit; 131, young seed. 132, 133, *C. pterophylla* (*Dickison 238*): 132, immature fruit; 133, seed. 134, *Pancheria robusta* (*Dickison 248*), young seed. 135, *Caldcluvia nymanii* (*Hoogland & Craven 11069*), mature seed. 136, *Acsmithia densiflora* (*Dickison 220*), seed coat. (C, cotyledon; EN, endosperm; EP, epidermis; IT, inner tegmen; P, papillae; S, sclerenchymatous layer; VB, vascular bundle.)

PLATE XVI

FIGURES 137–145. Structure of fruits and seeds in Cunoniaceae. 137–140, *Aistopetalum multiflorum* (*Hoogland & Craven 10826*): 137, immature fruit, transverse section; 138, immature fruit, longitudinal section; 139, hilar end of young seed, transverse section; 140, chalazal end of young seed, transverse section. 141, 142, *Schizomeria ovata* (*Hoogland 11684*), transverse sections: 141, young seed; 142, outer portion of seed coat. 143, *Anodopetalum biglandulosum* (*Webb 3337*), inner region of pericarp, transverse section. 144, 145, *Codia nitida* (*Dickison 221*), transverse sections: 144, fruit; 145, pericarp. (CR, crystalliferous layer; E, endocarp; EP, epidermis; IT, inner tegmen; S, sclerenchymatous layer; VB, vascular bundle.)

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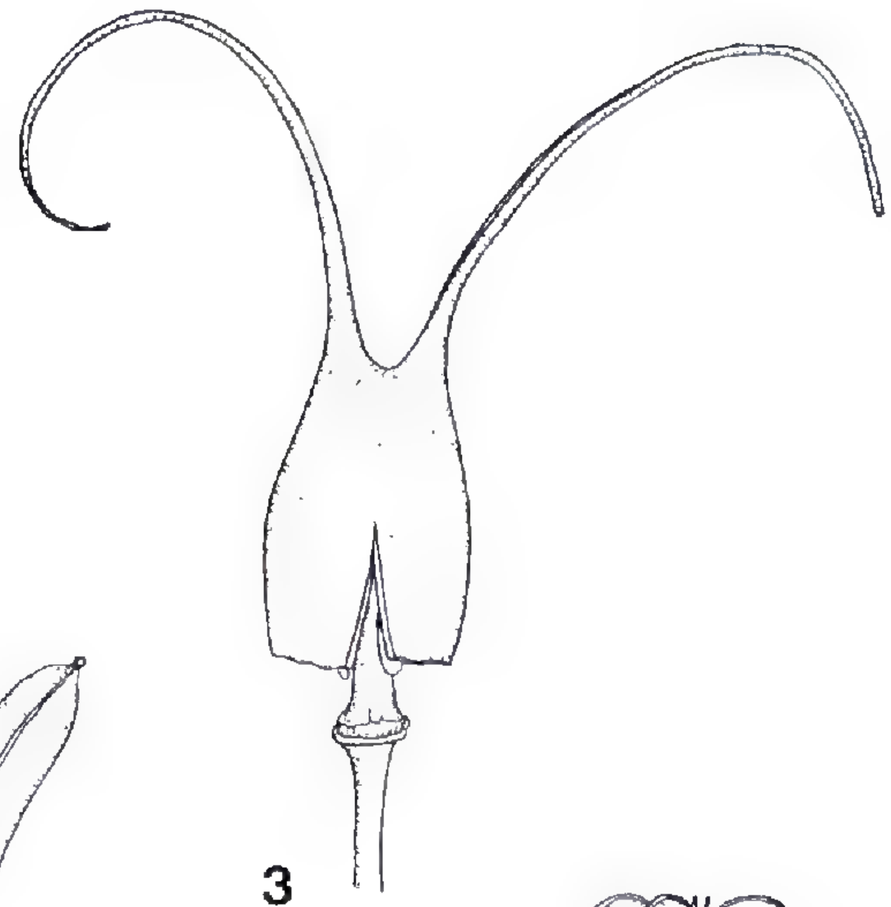

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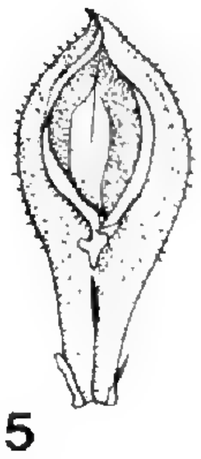

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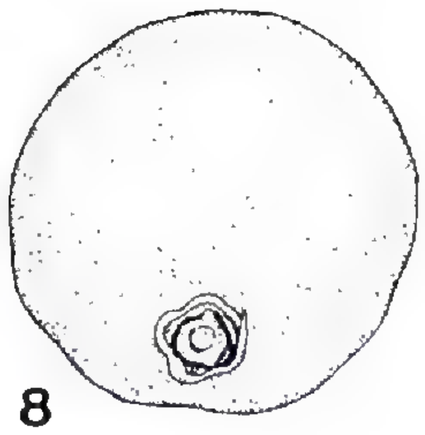

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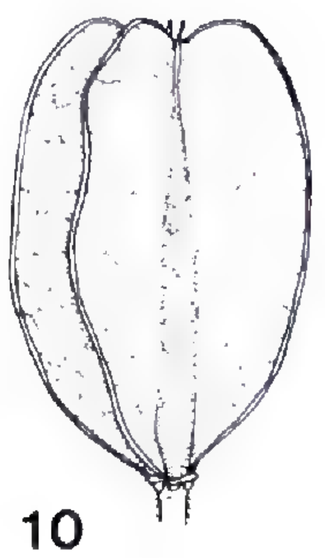

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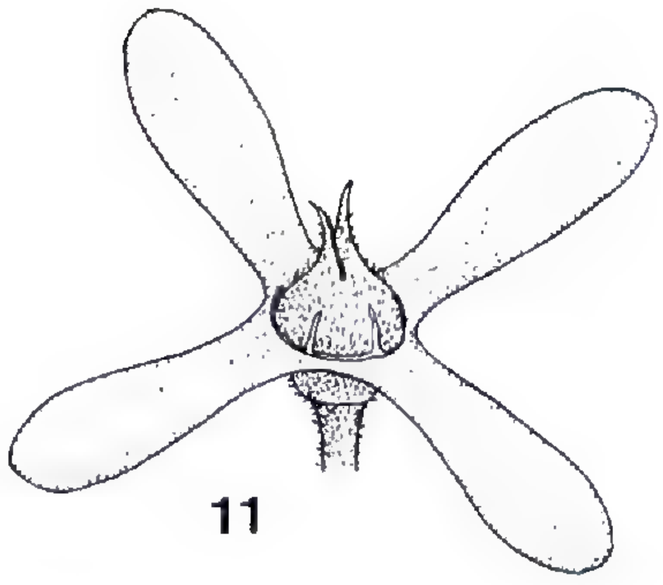

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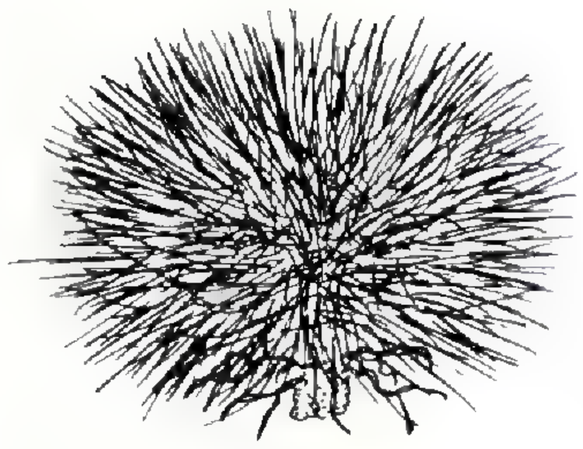

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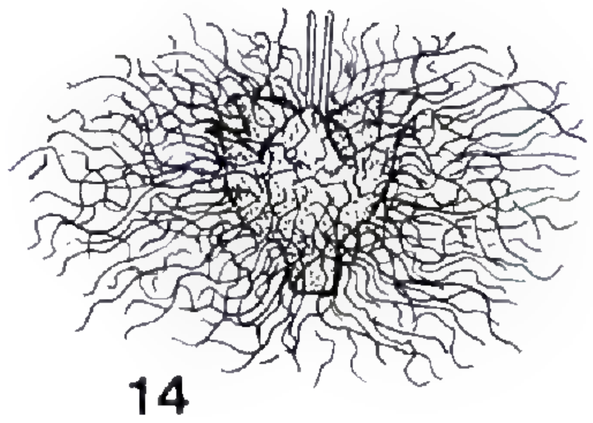

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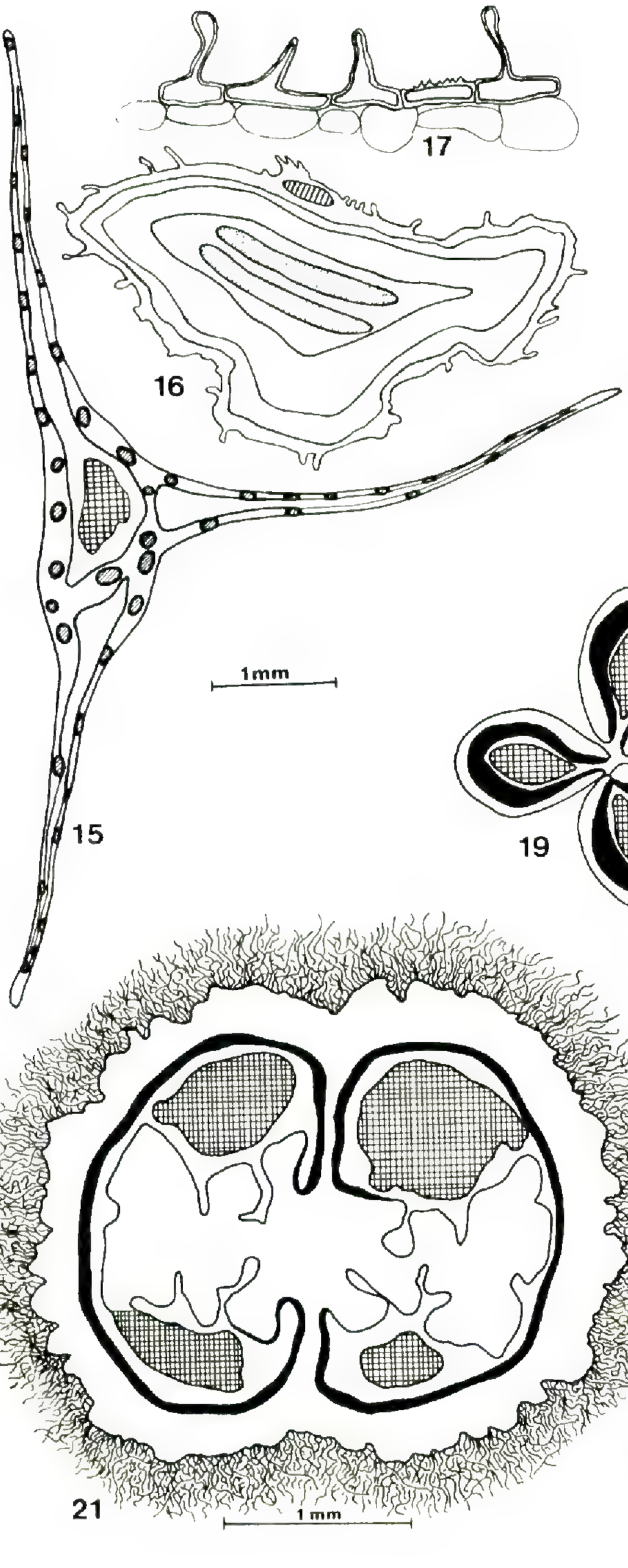
PLATE I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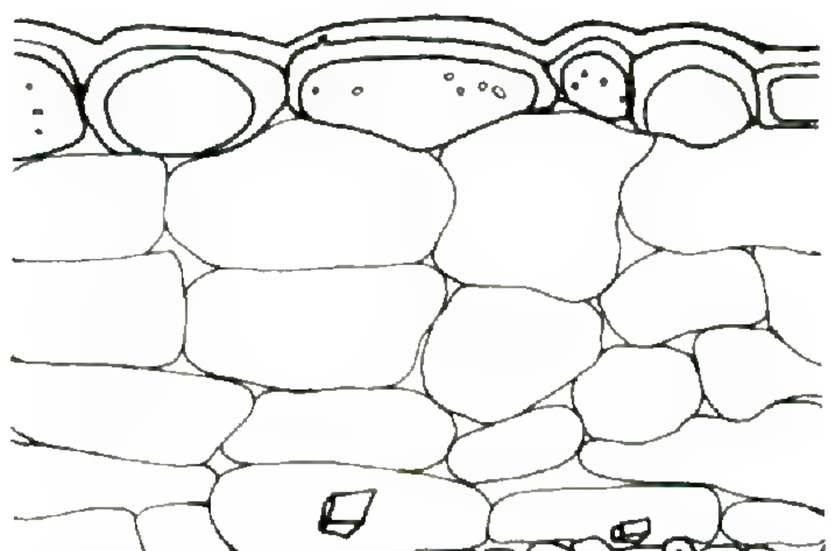
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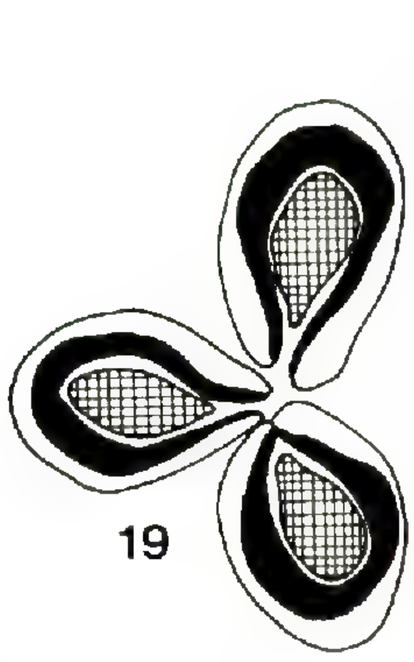
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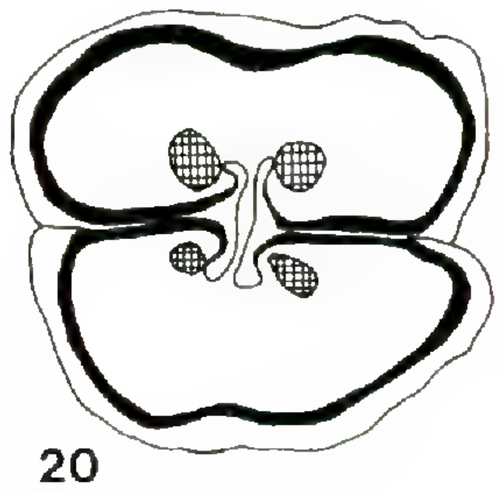
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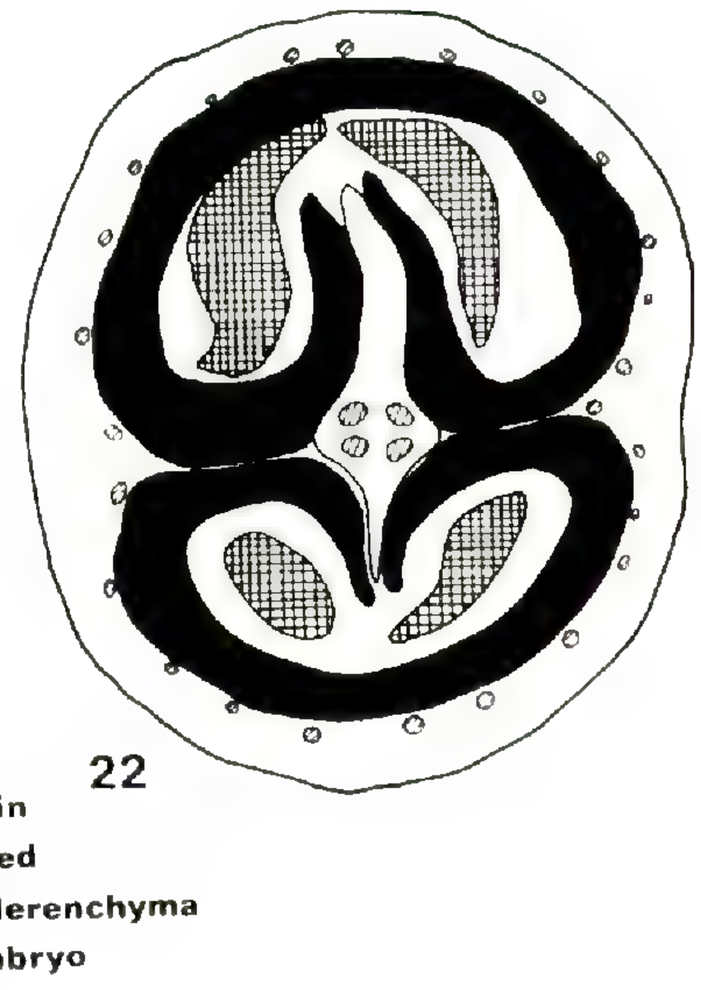
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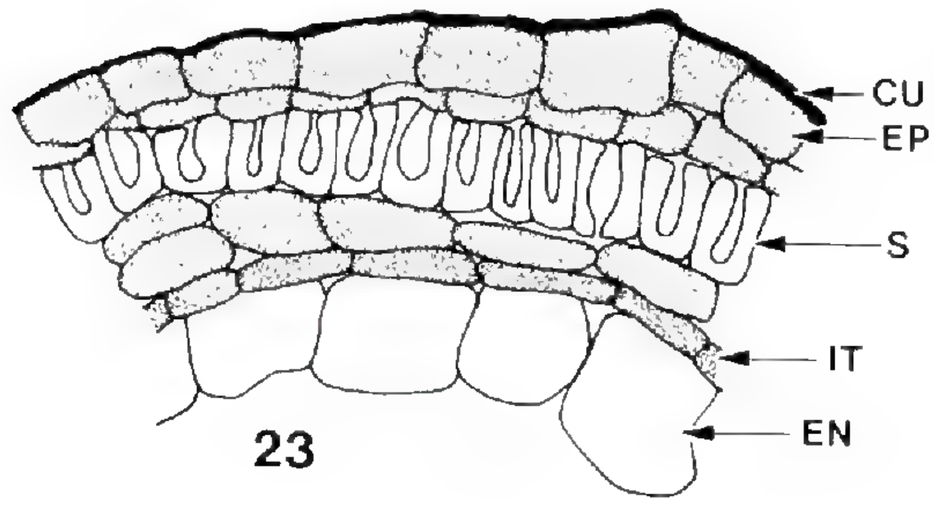
= seed
= sclerenchyma
= embryo

PLATE II



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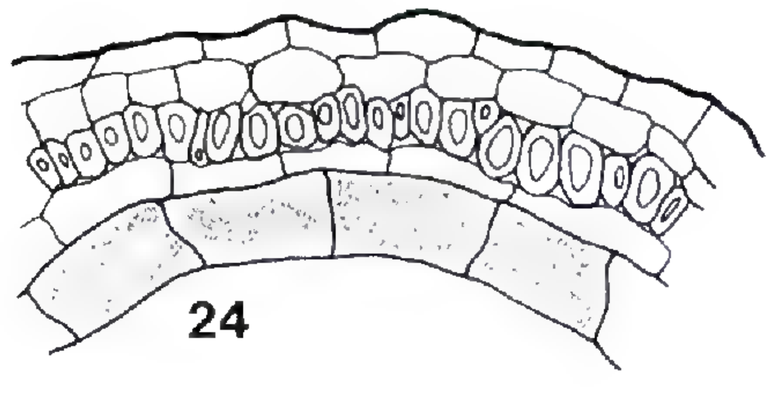
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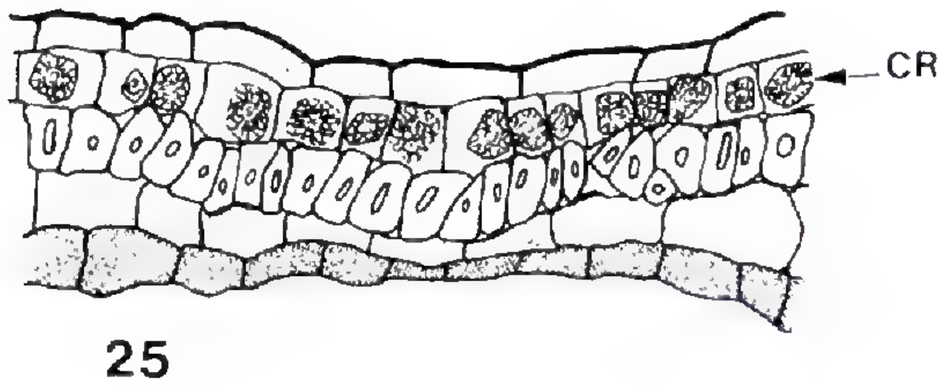

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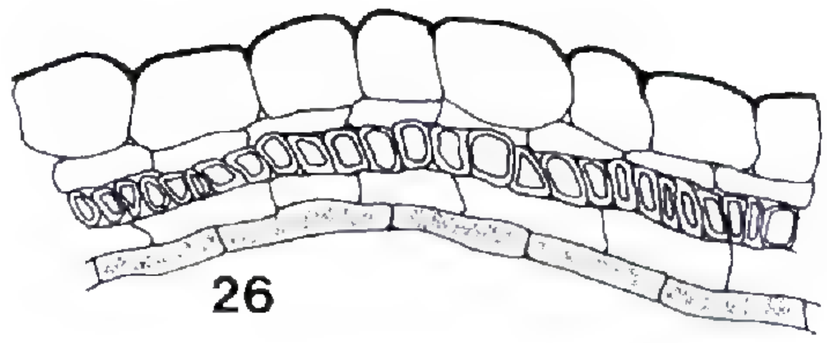
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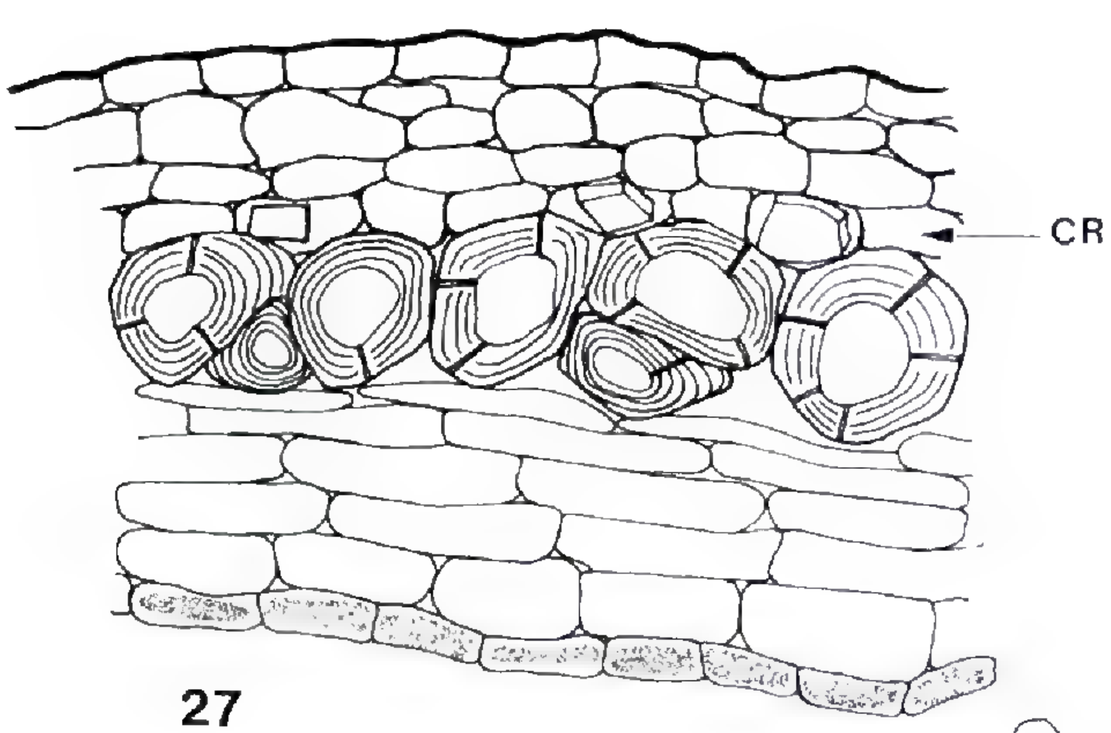

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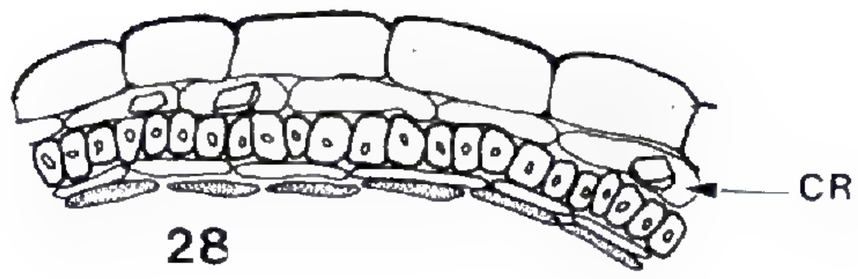

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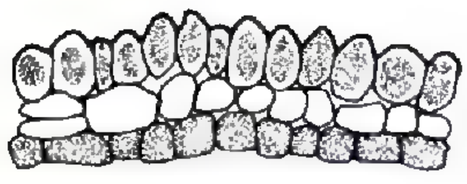
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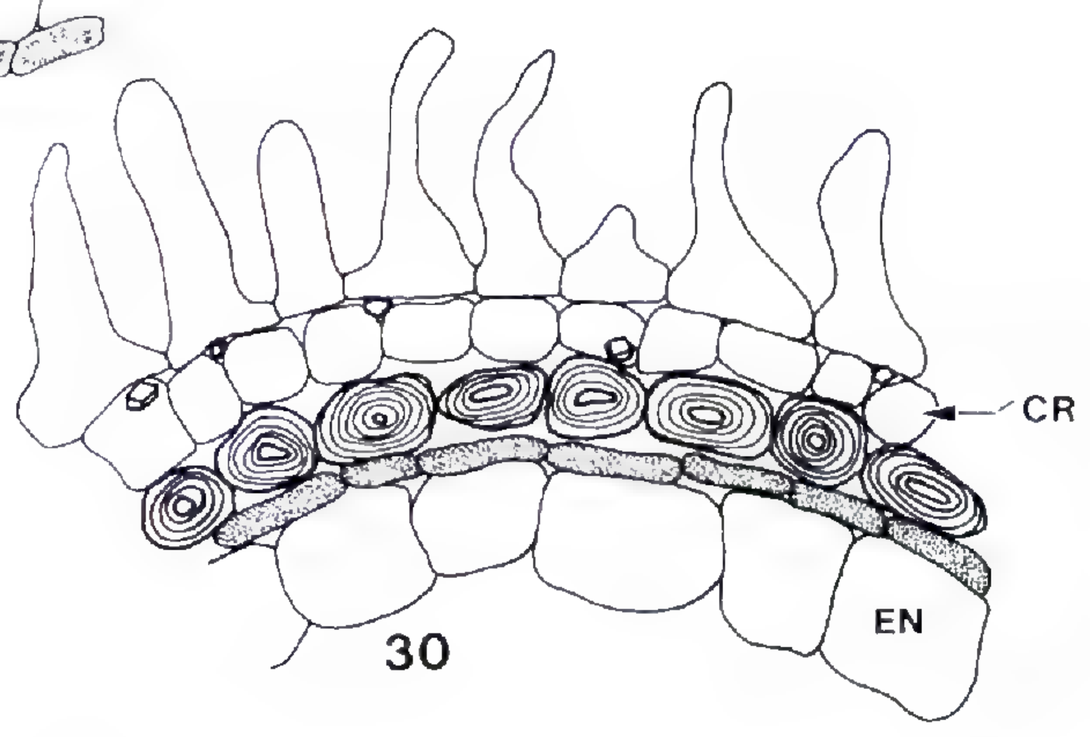

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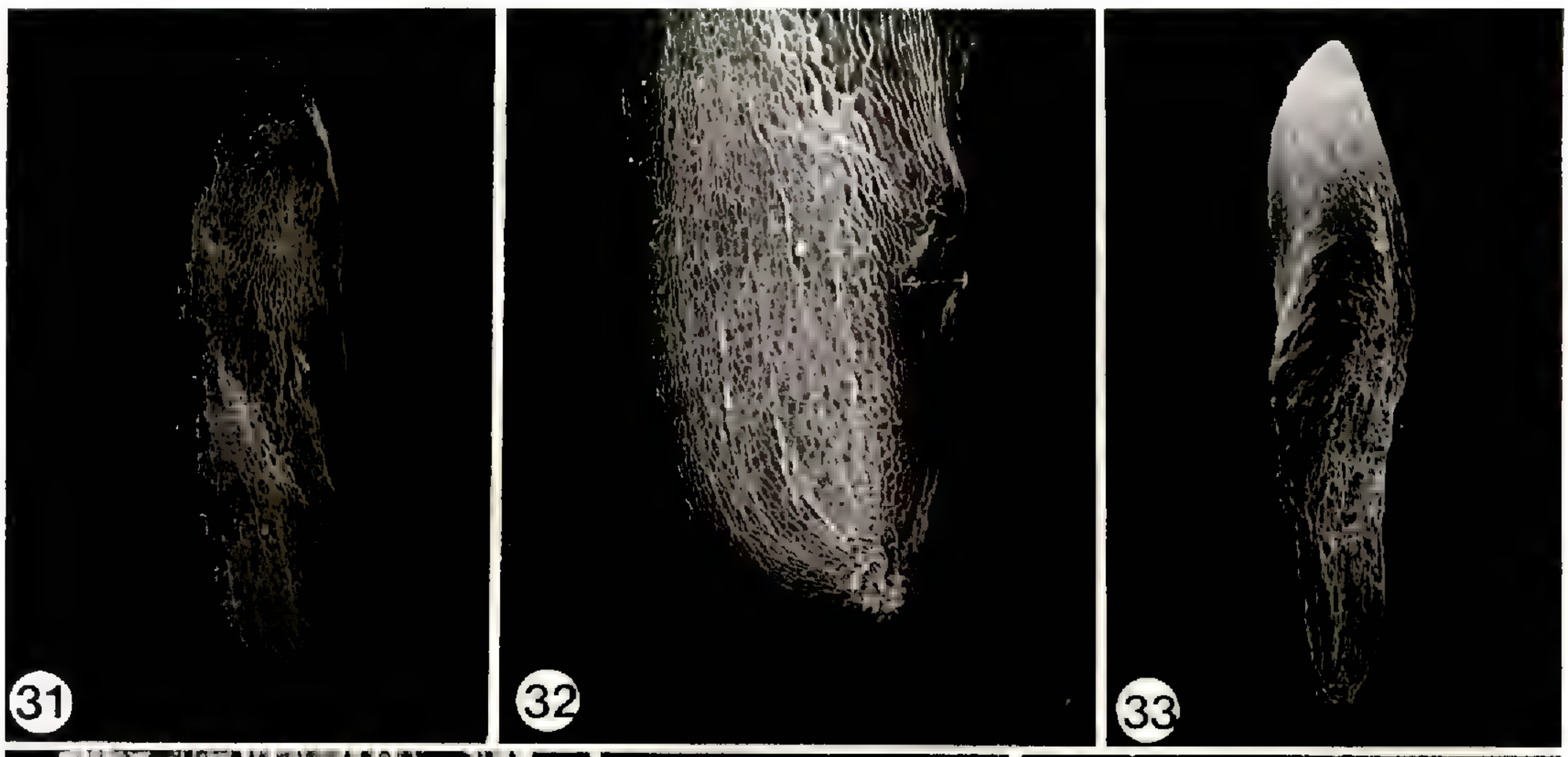

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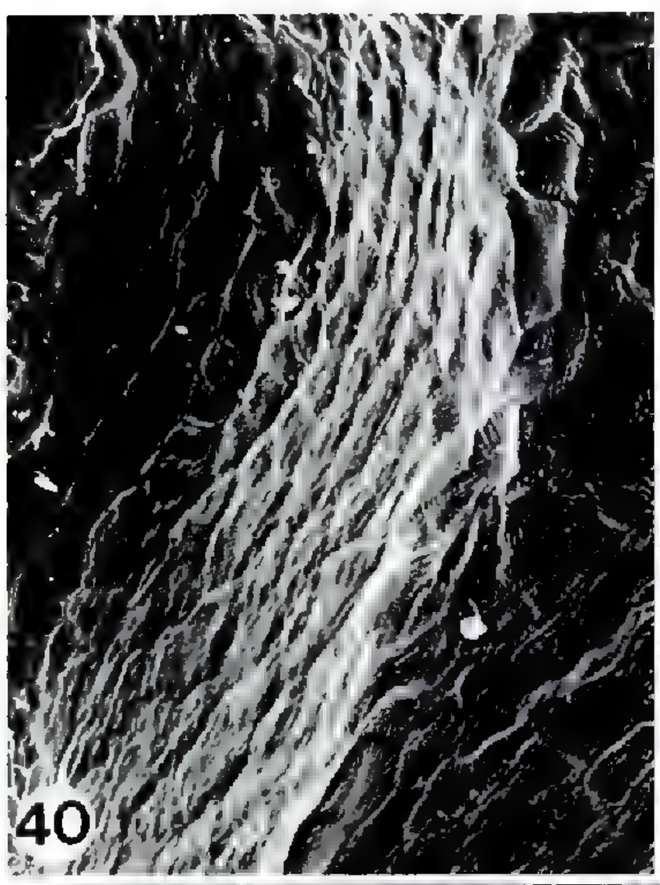

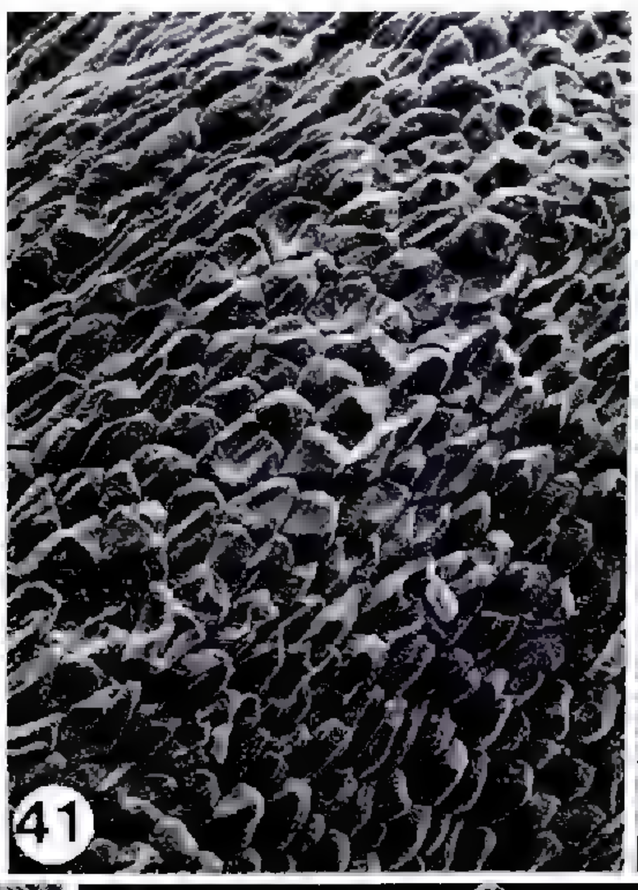

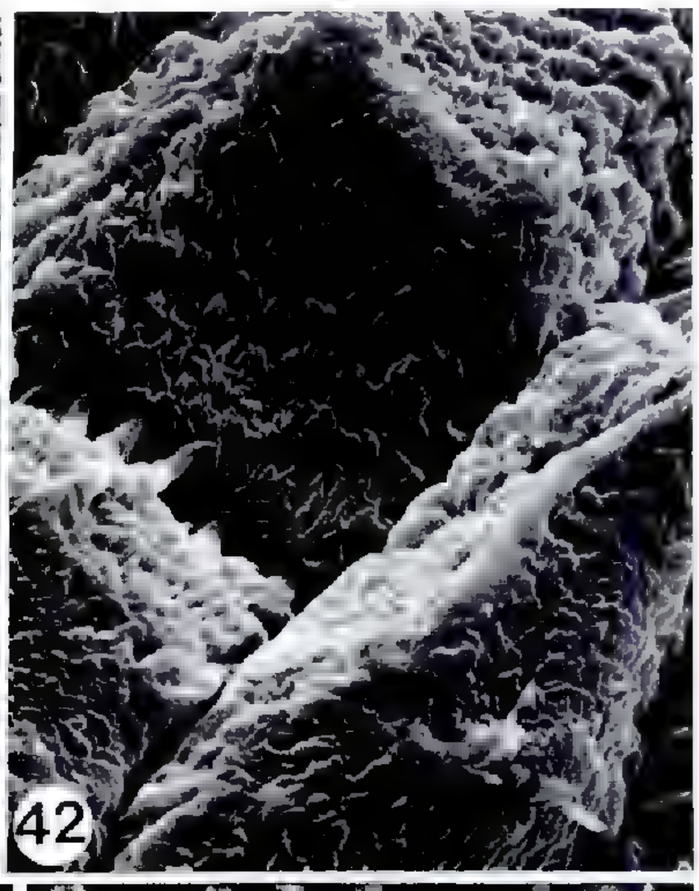

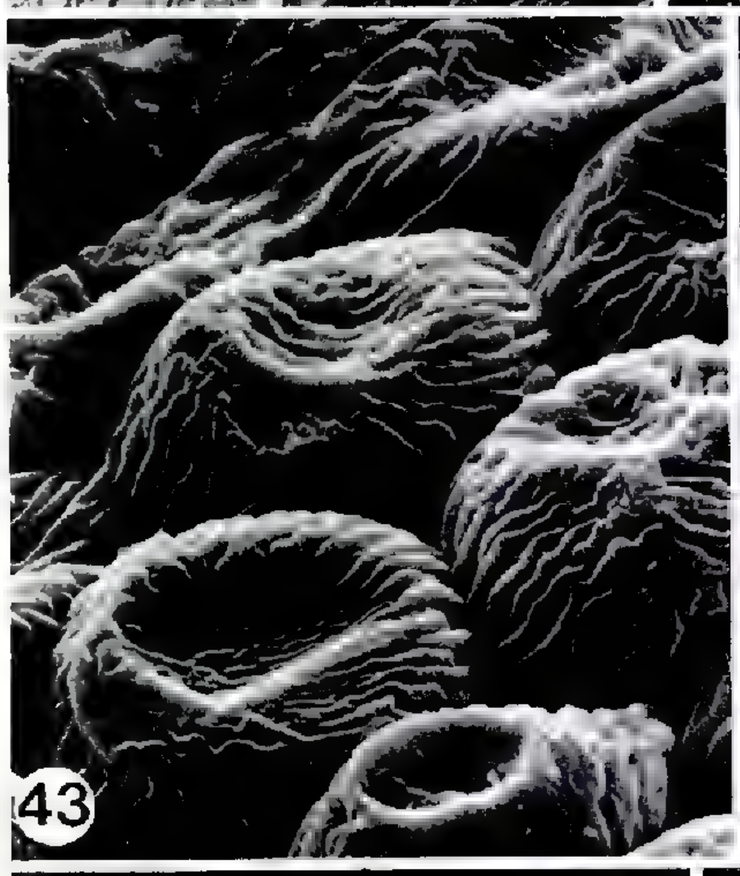

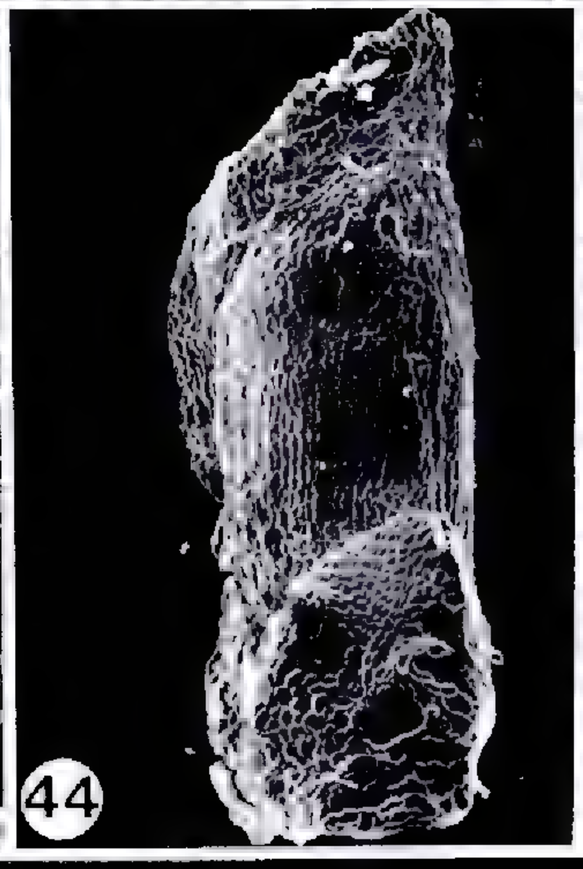

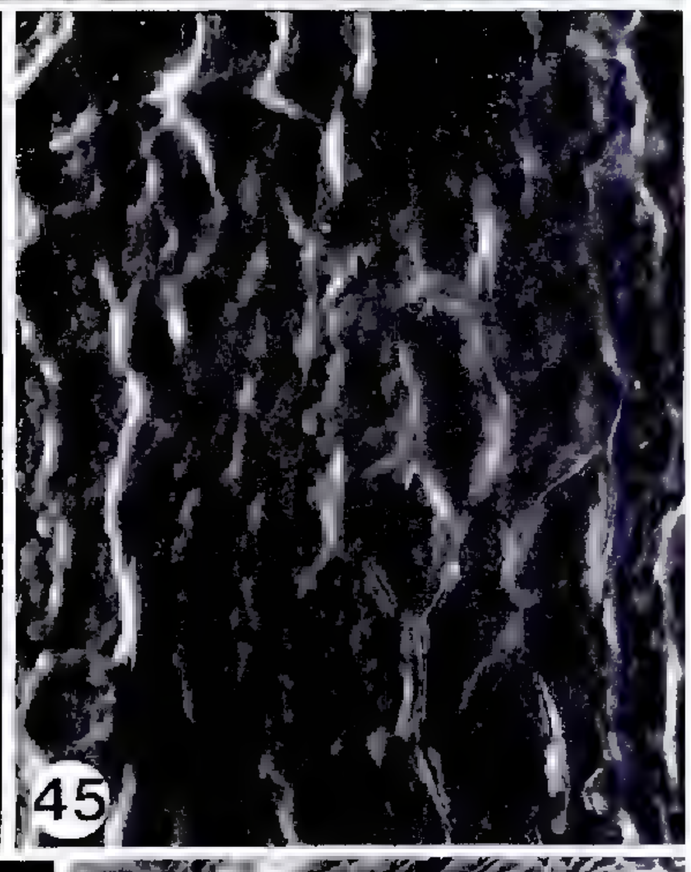

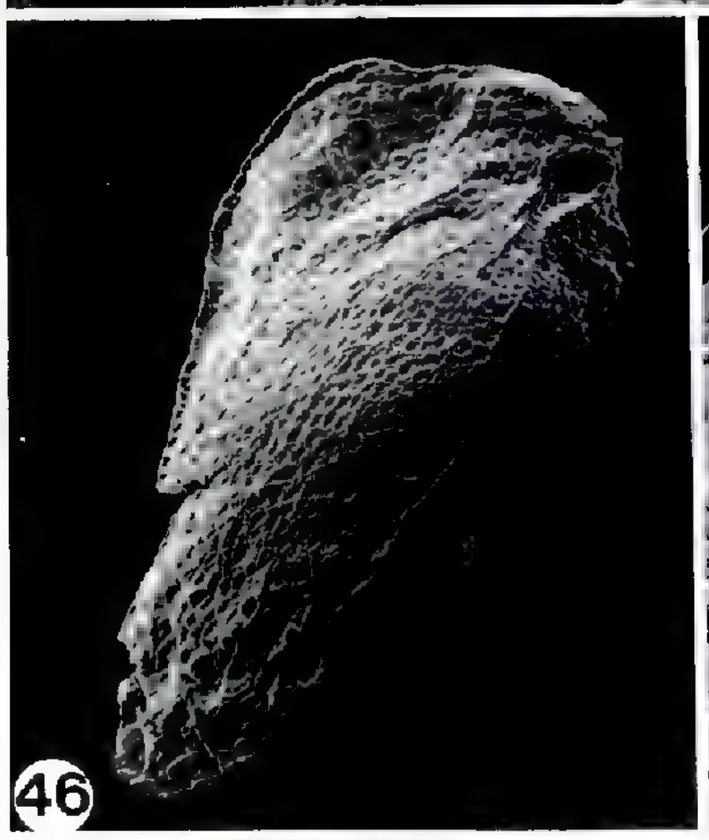

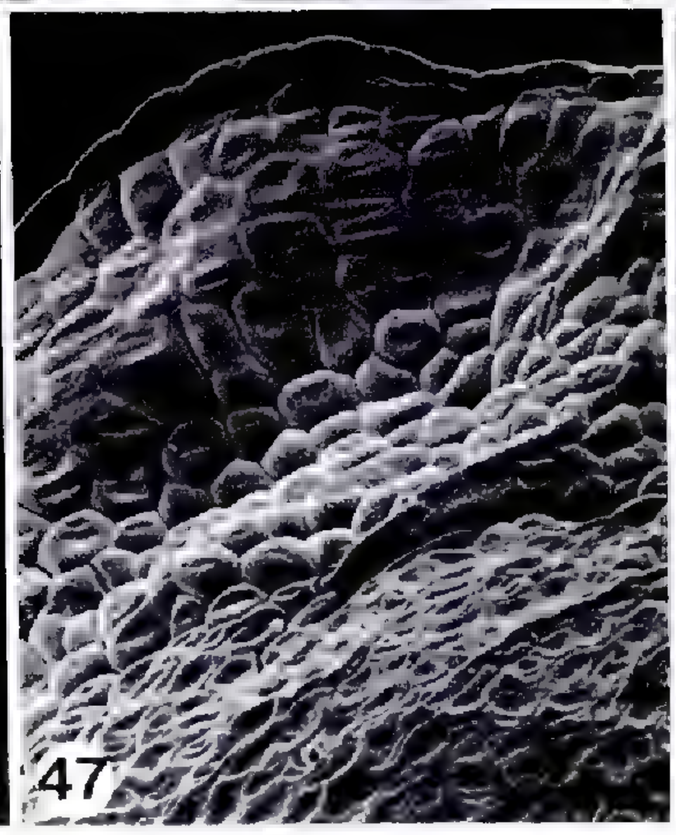

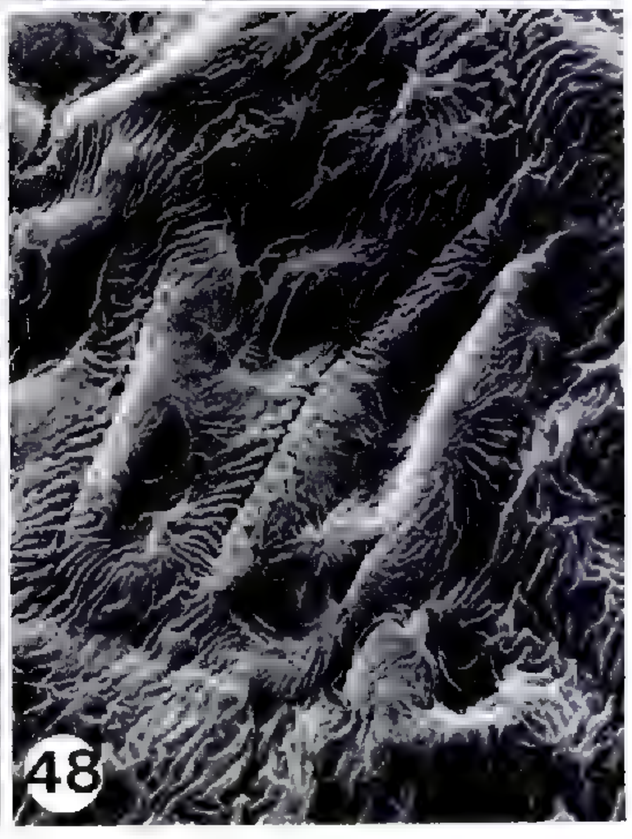

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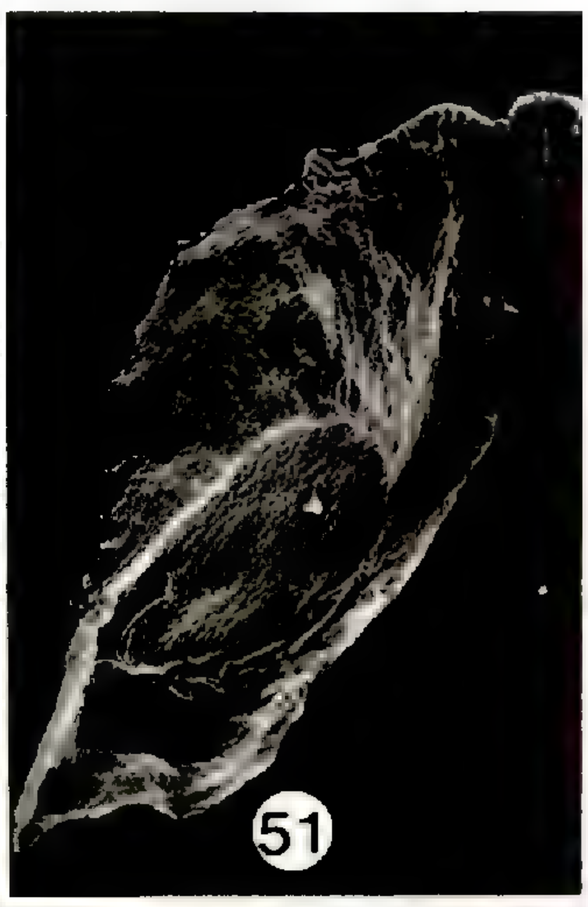

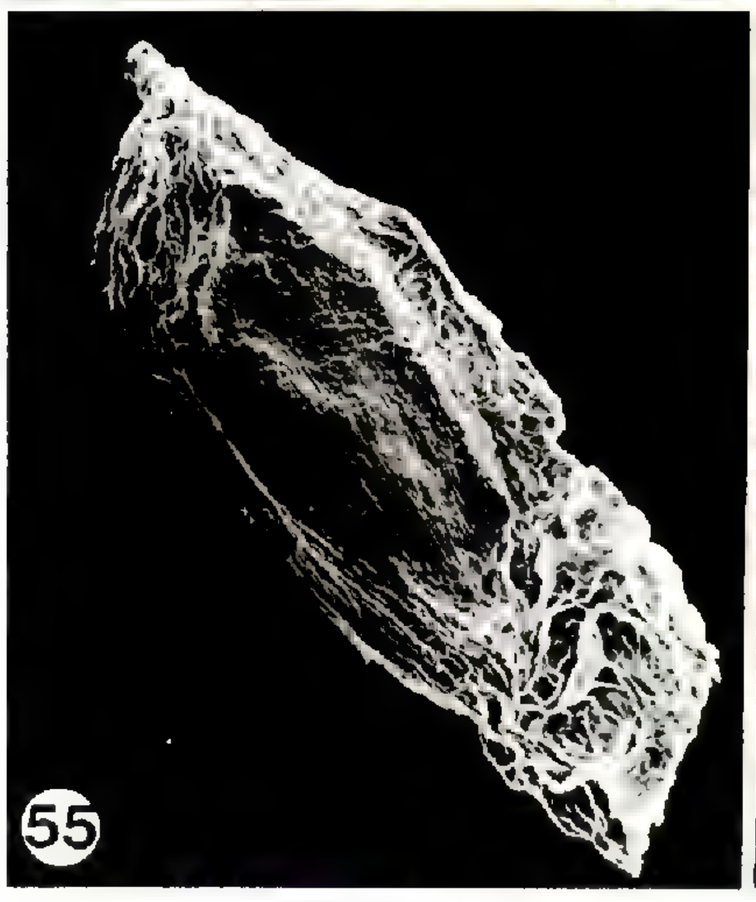

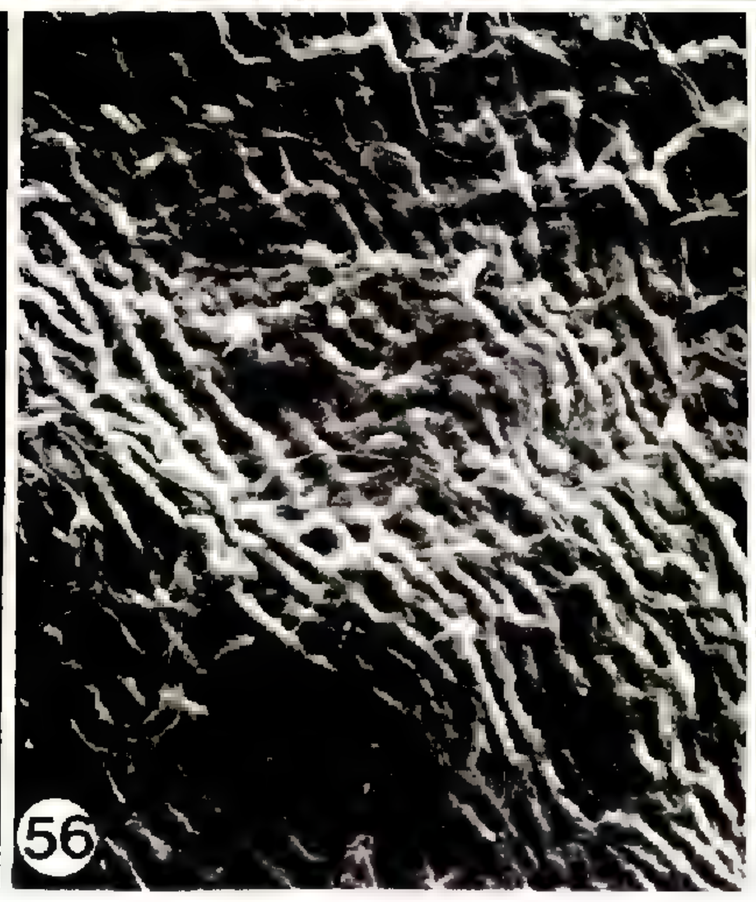

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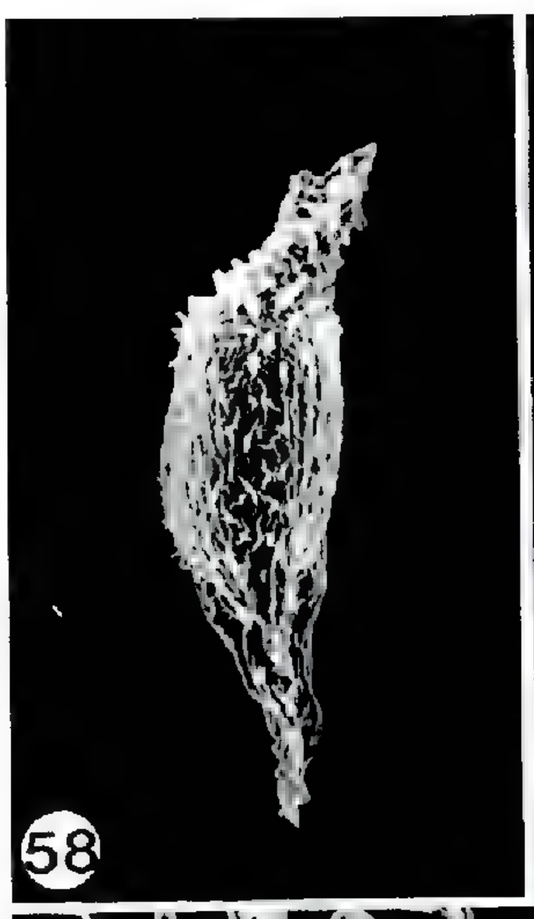

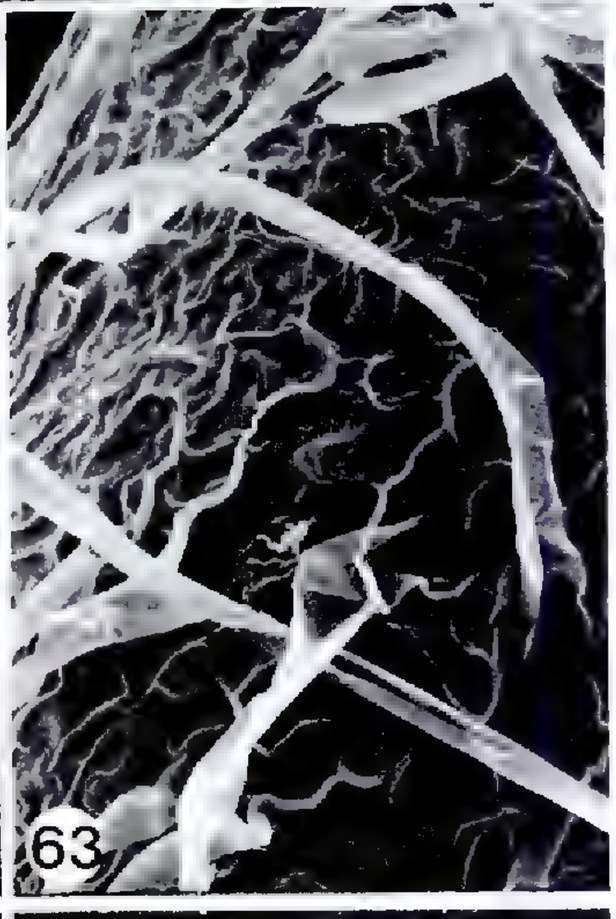

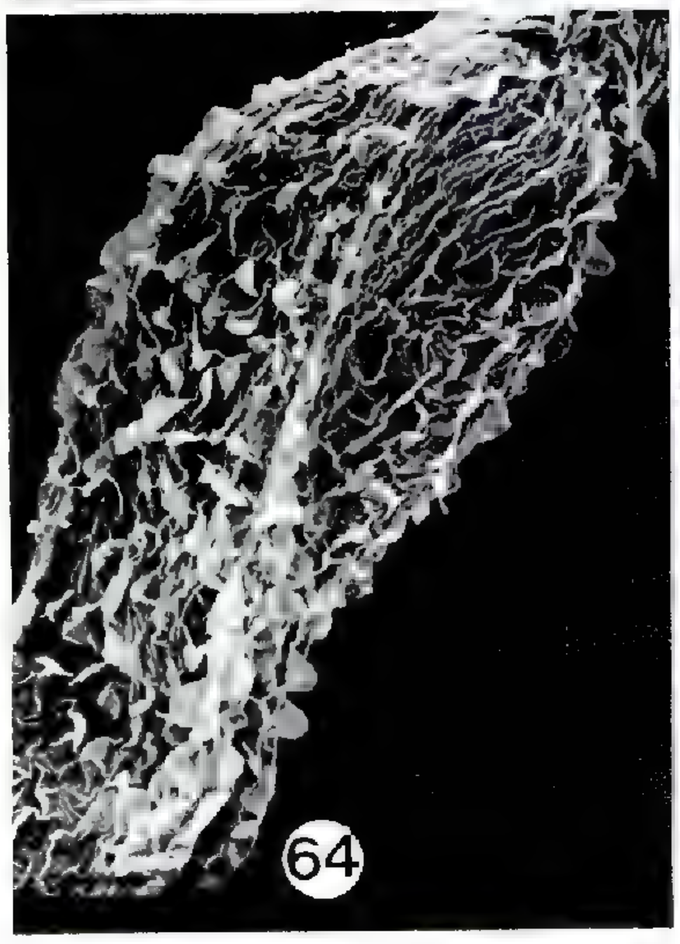

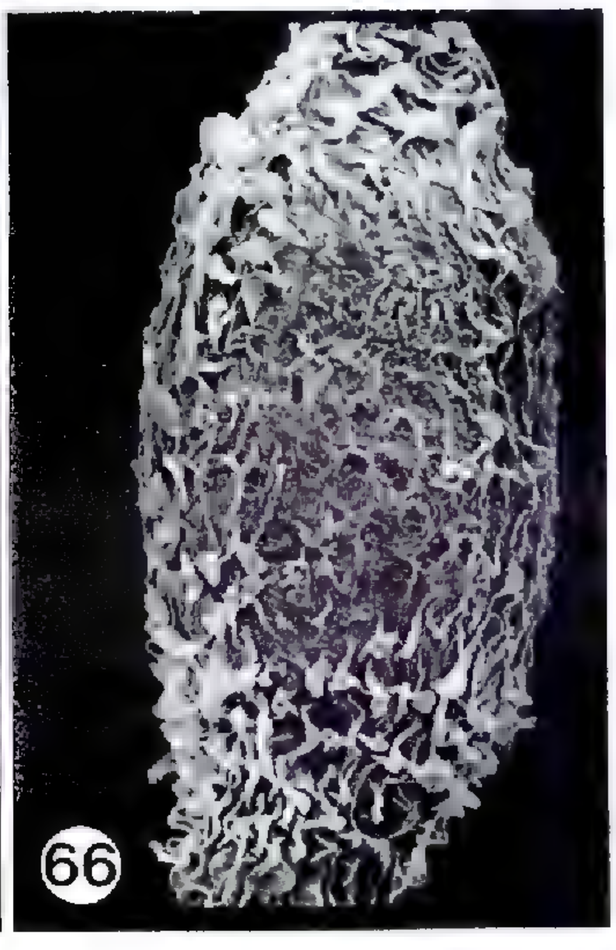

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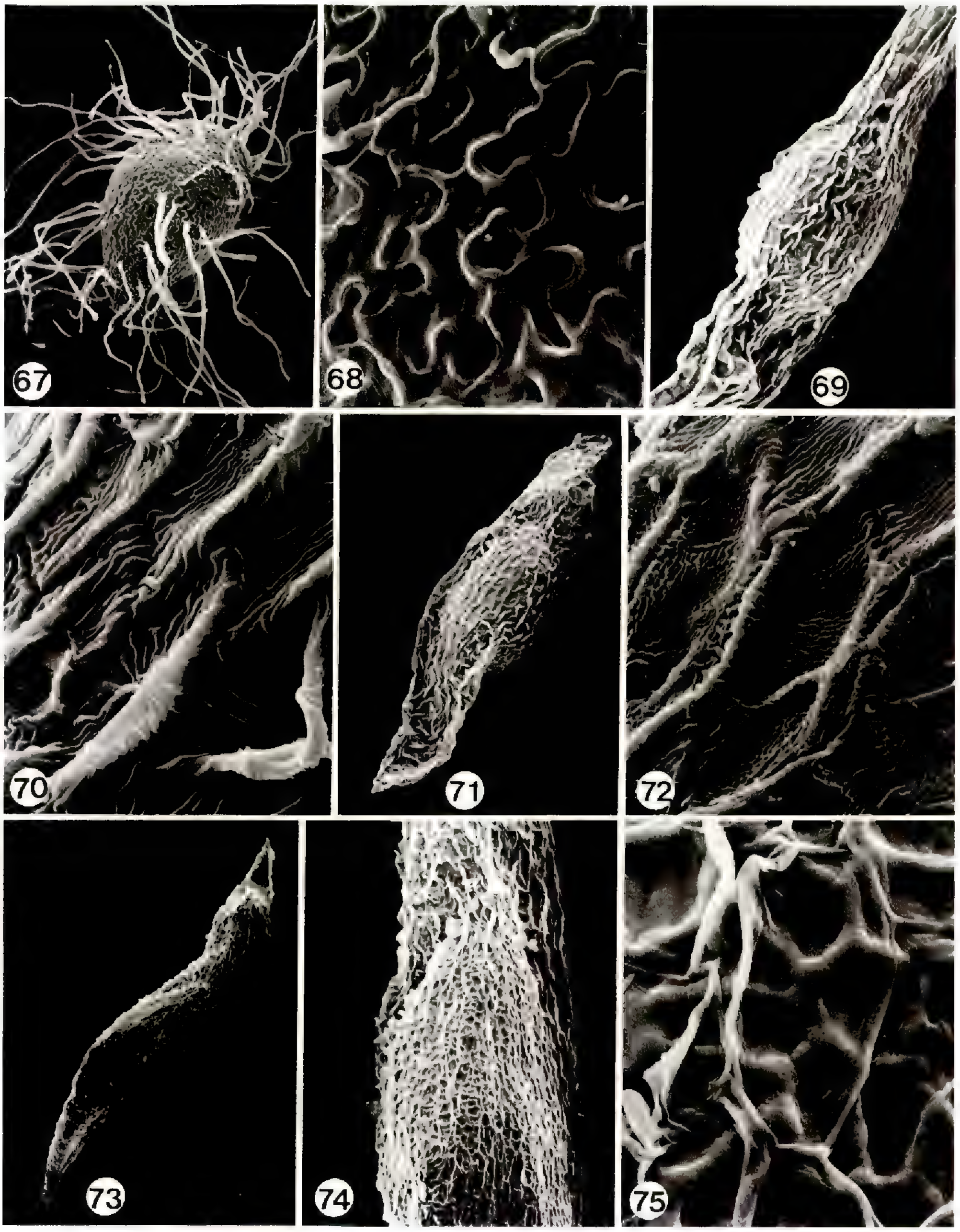

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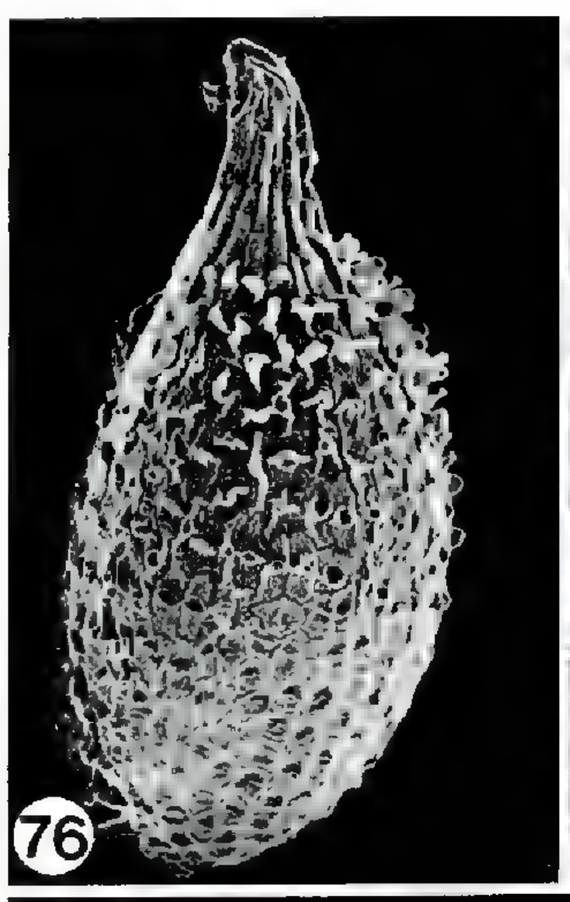

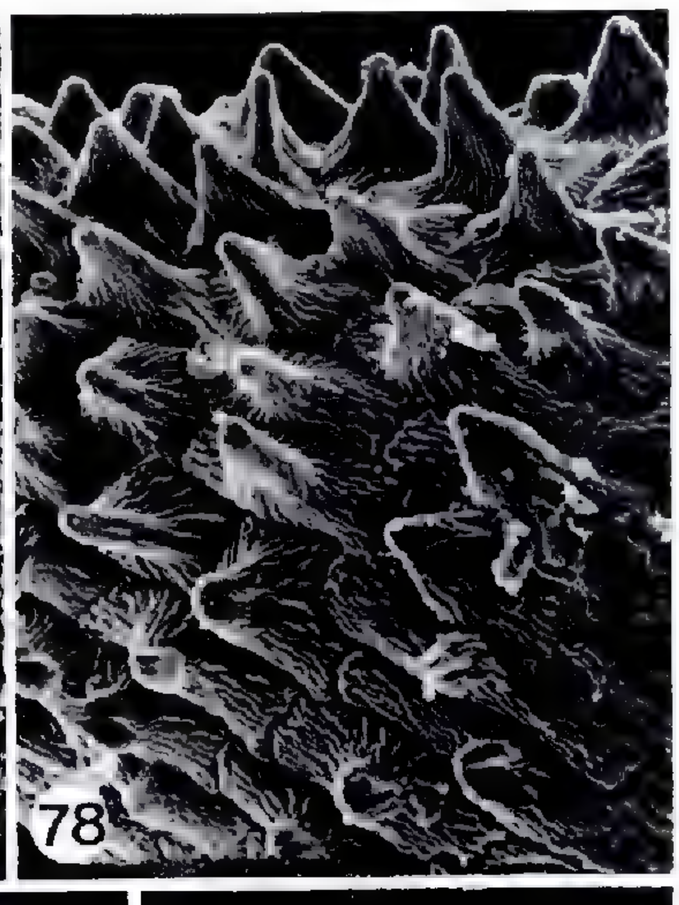

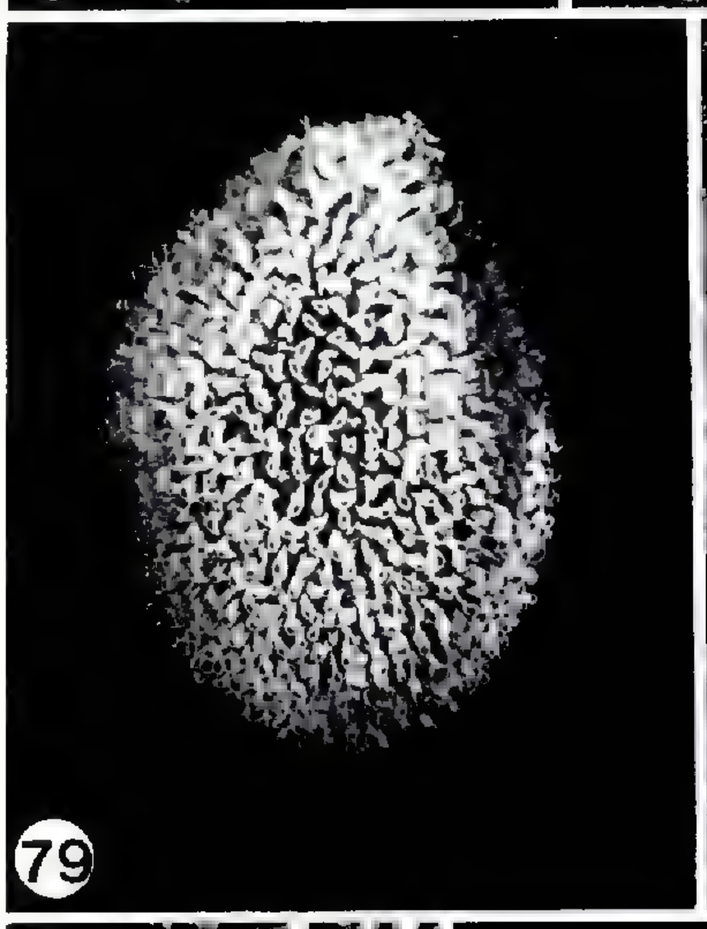

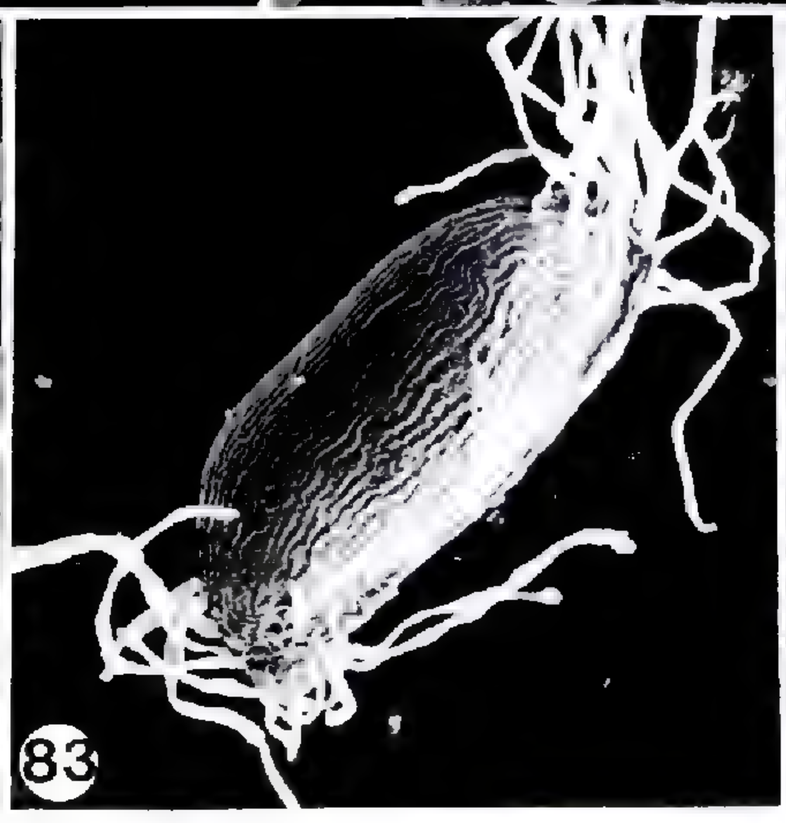

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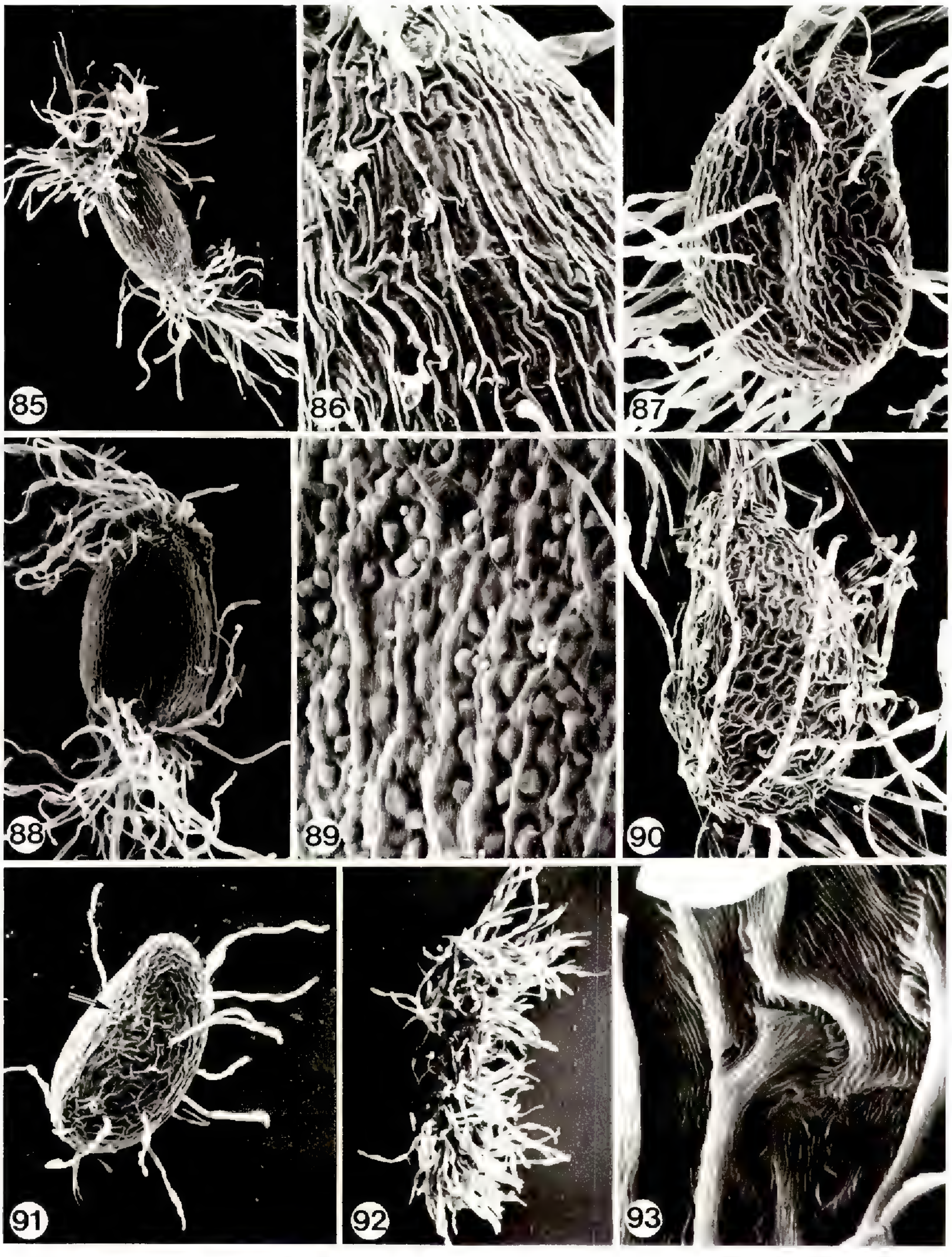

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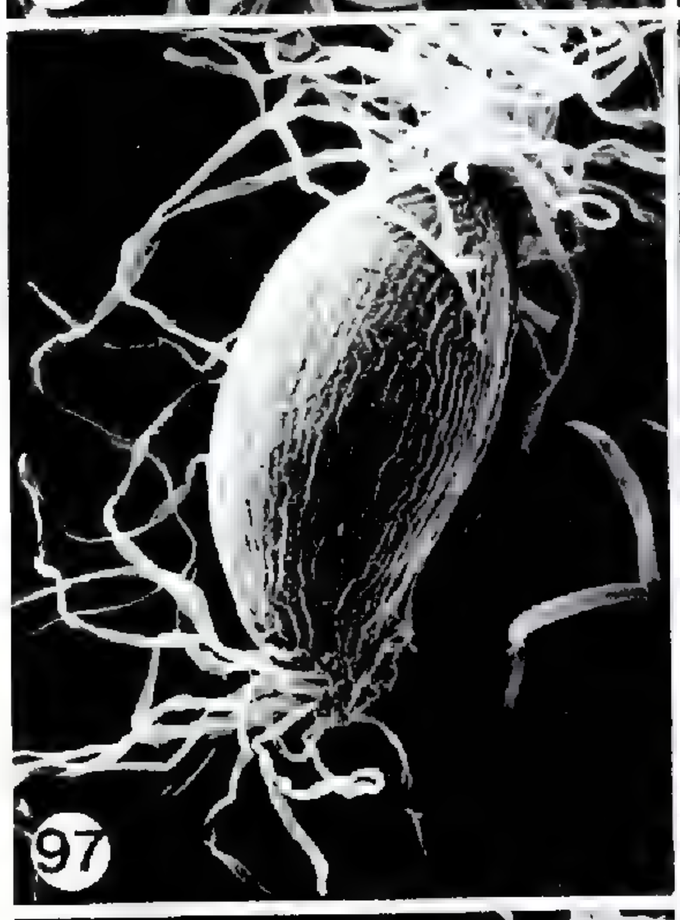

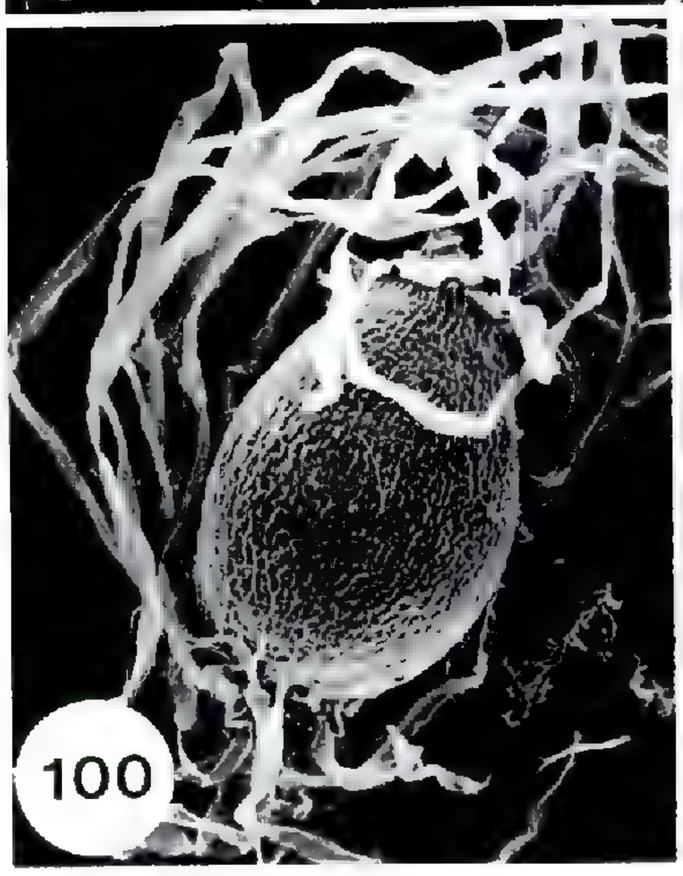

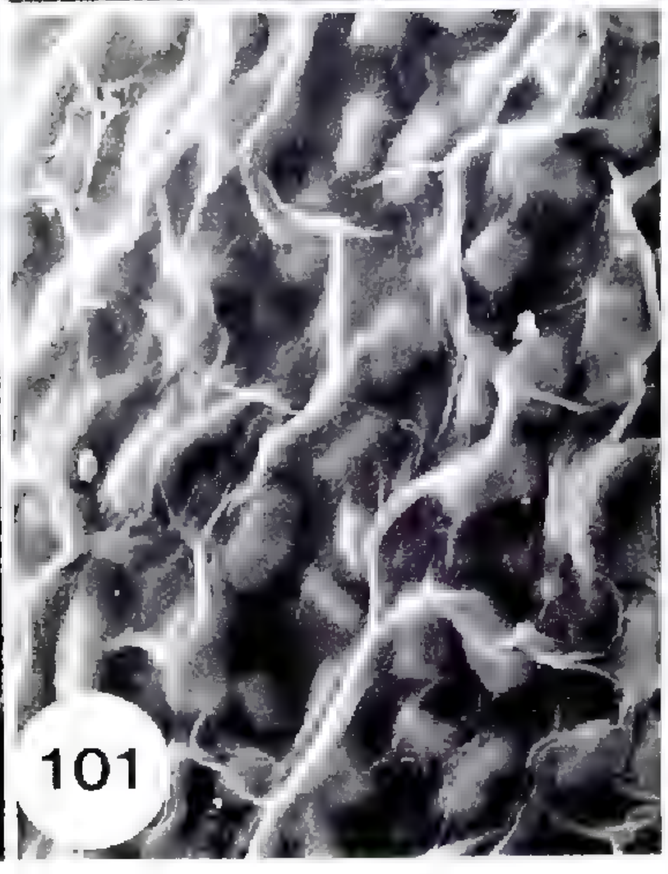

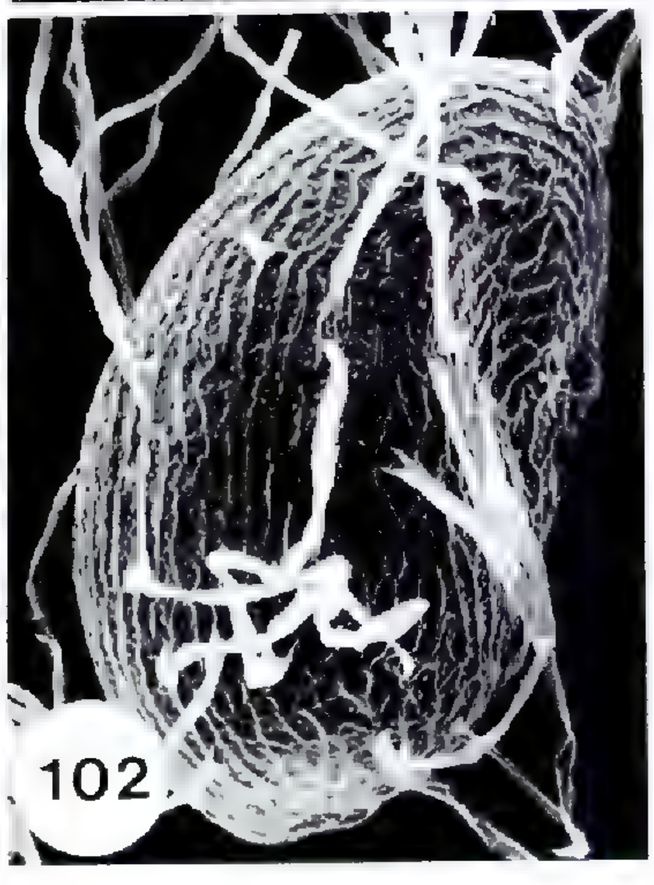

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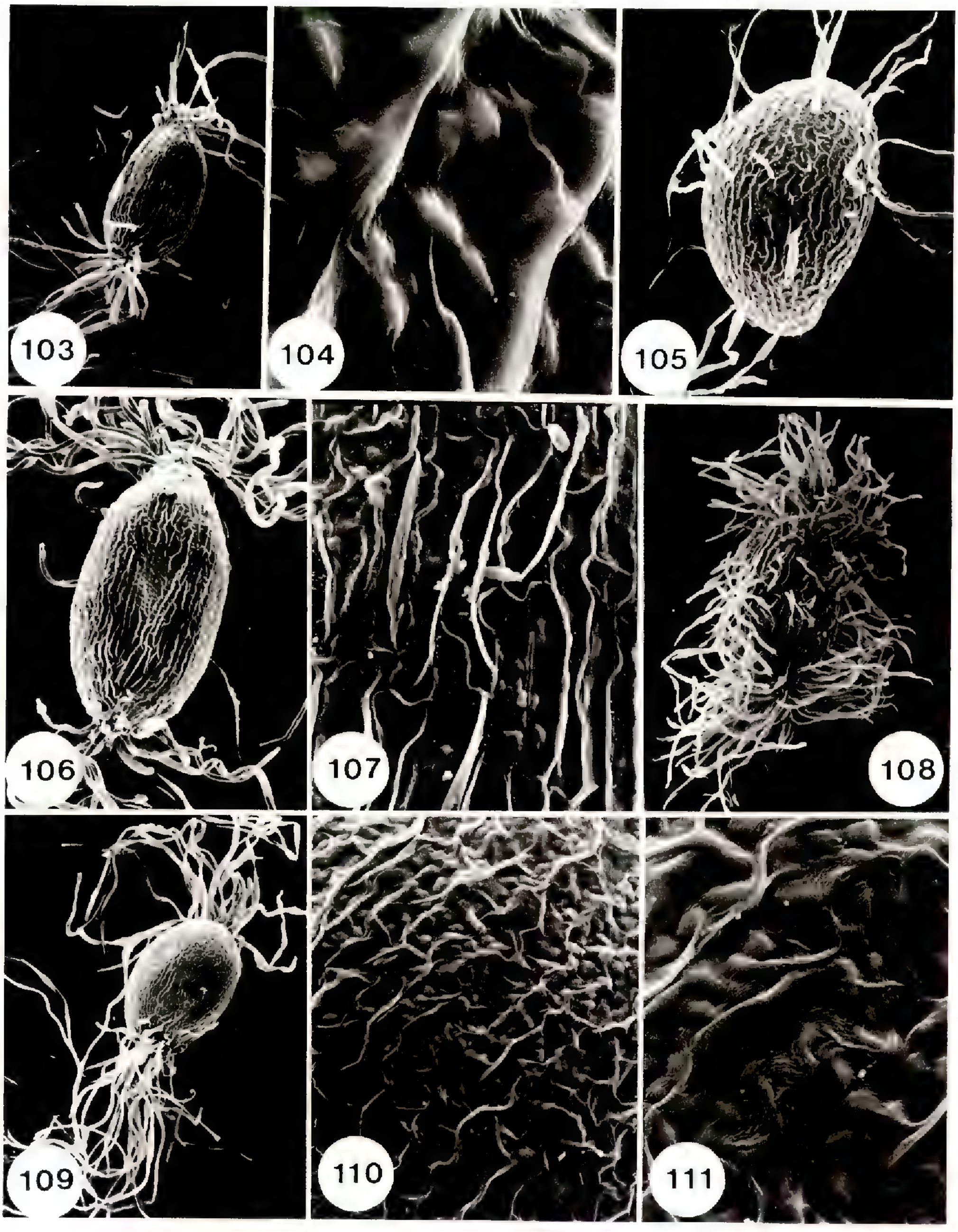

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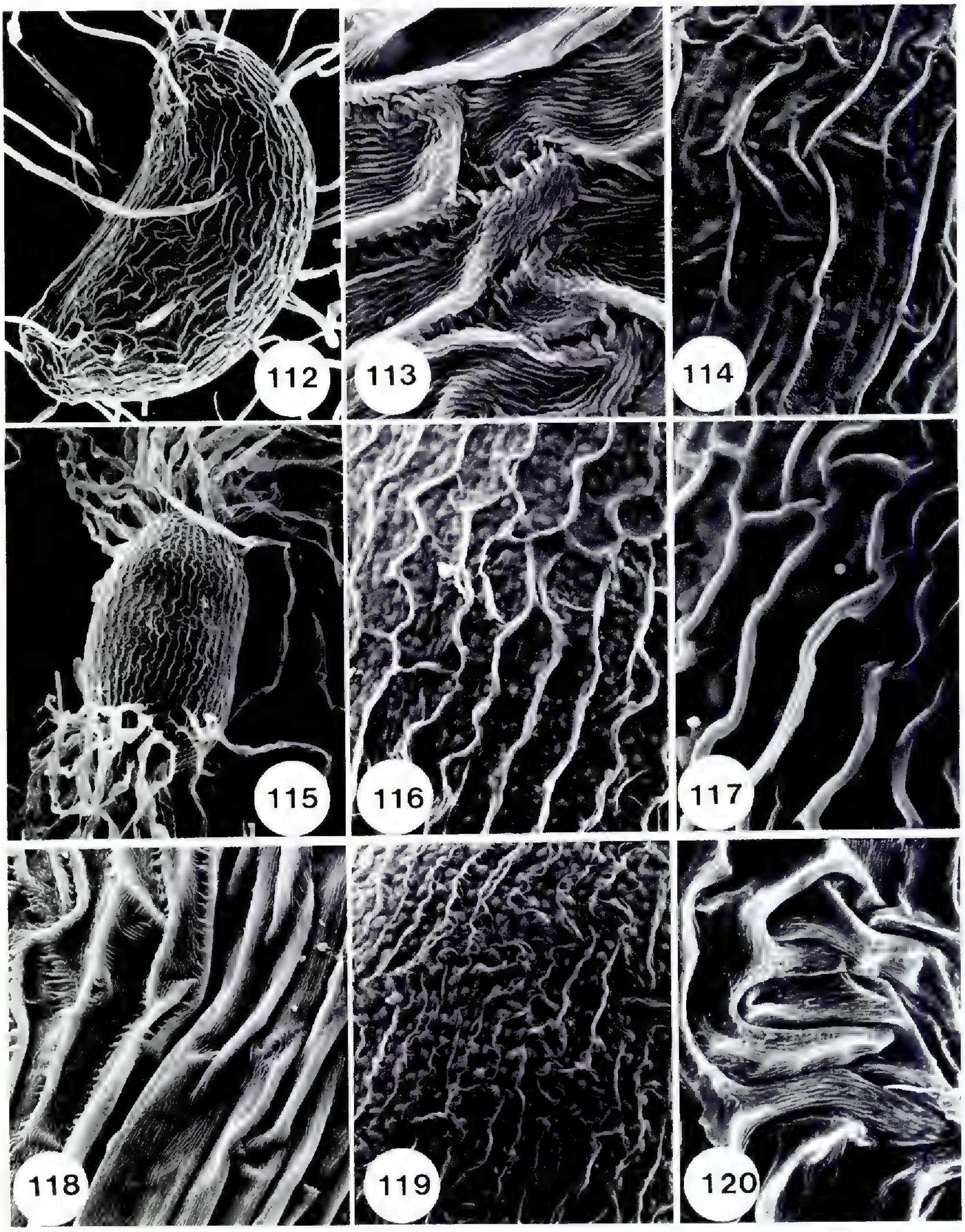

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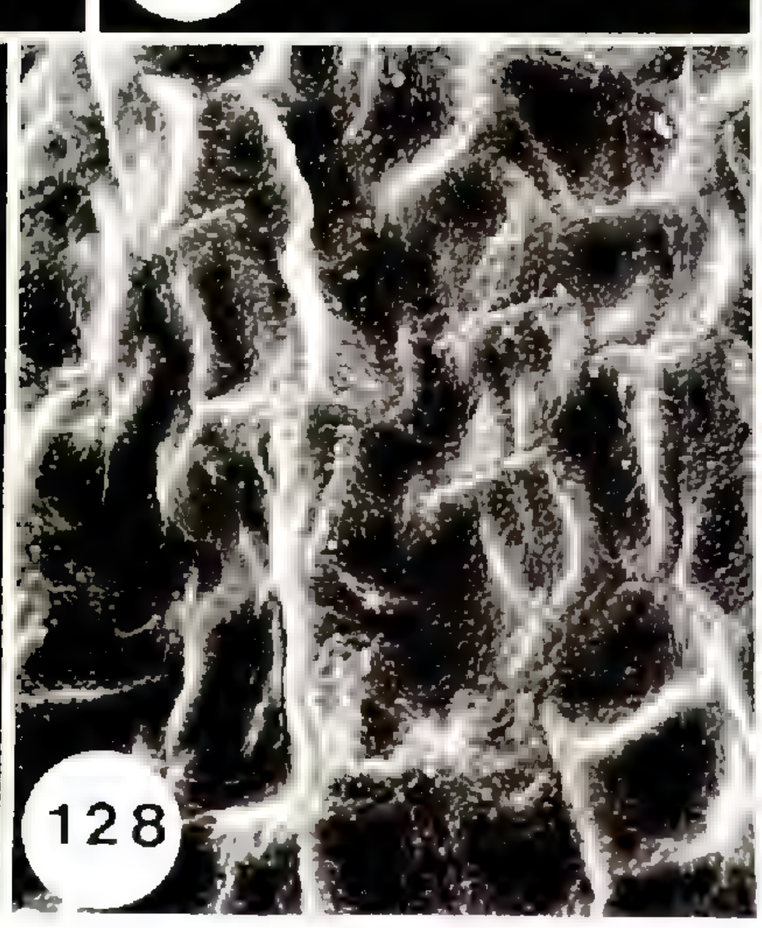

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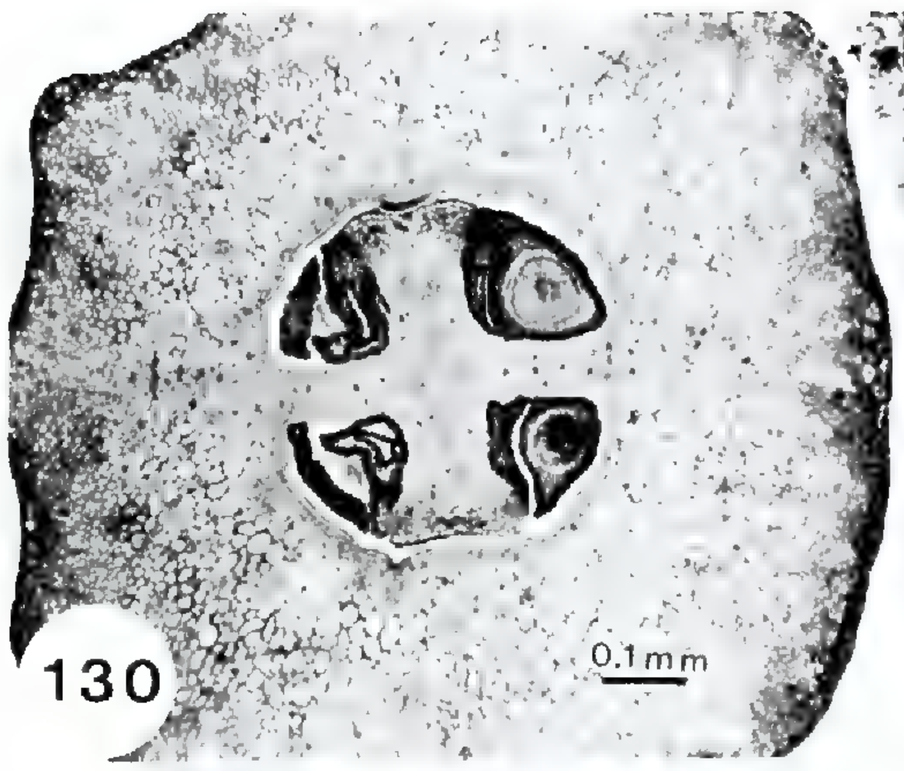

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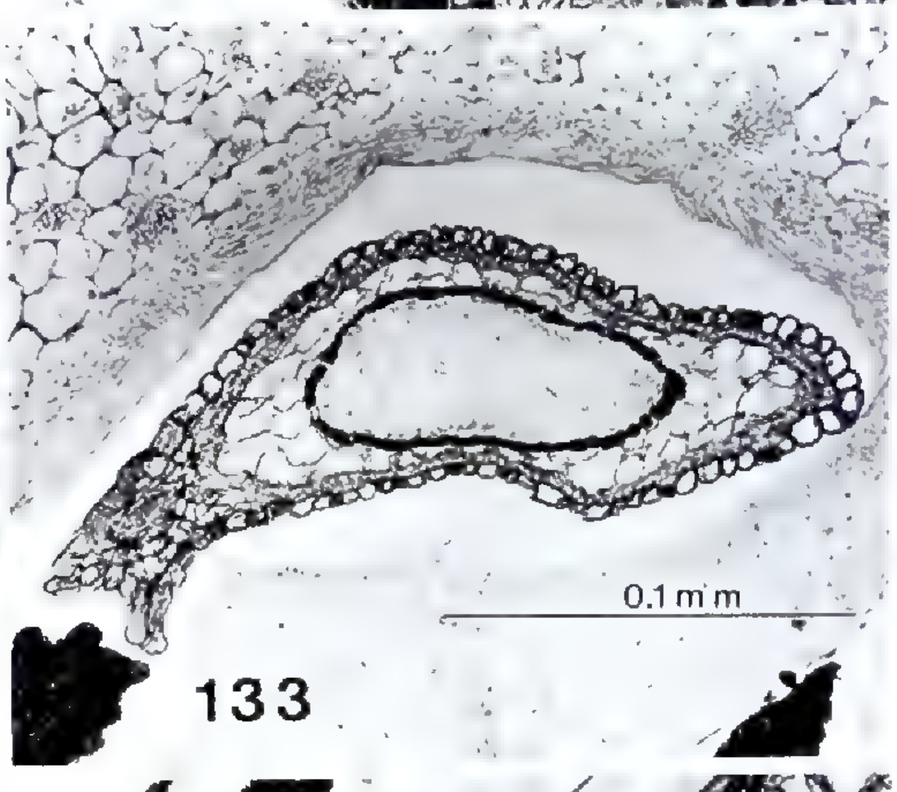

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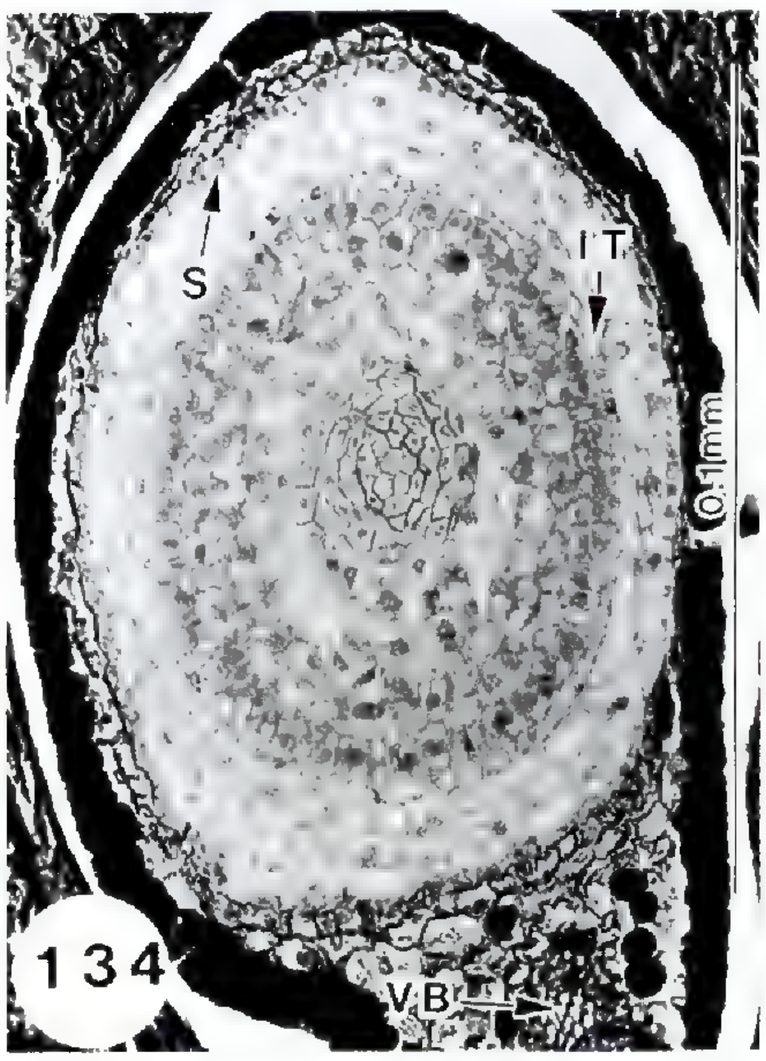

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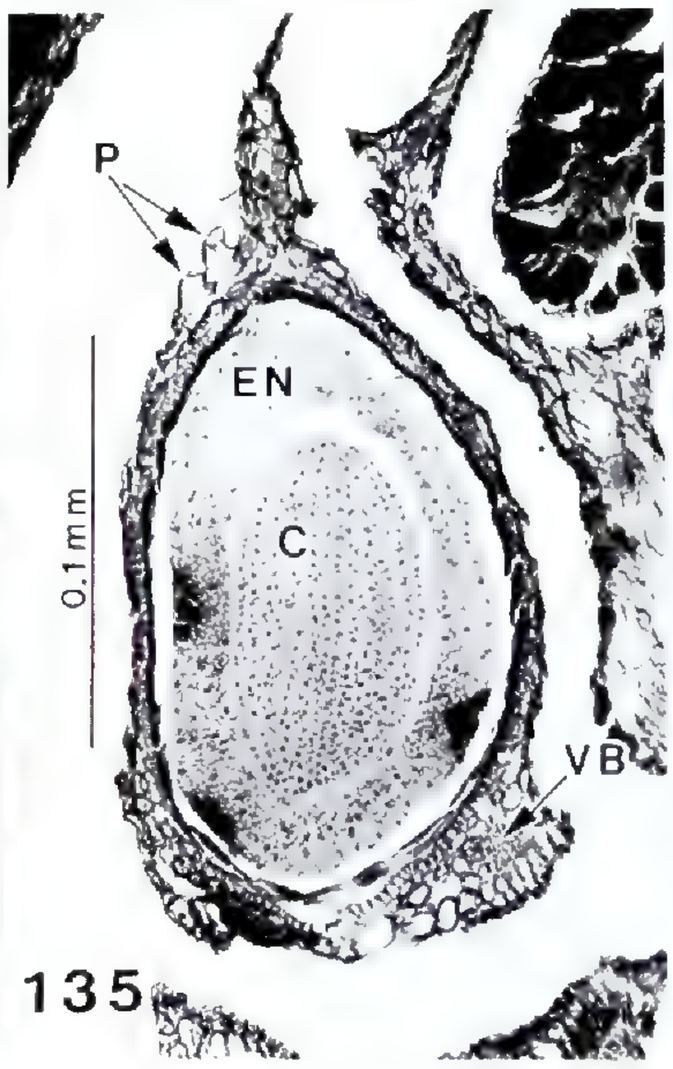

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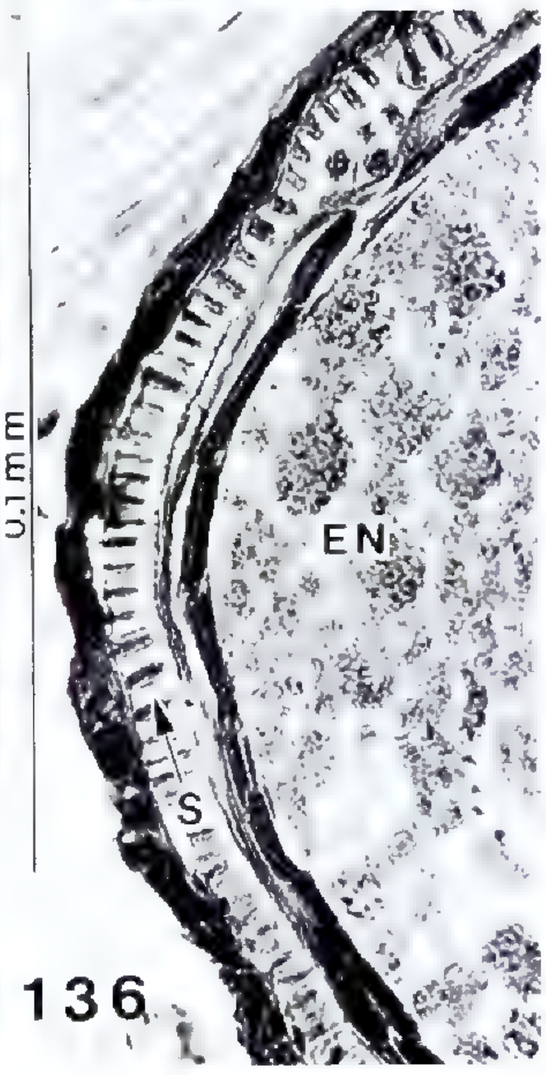

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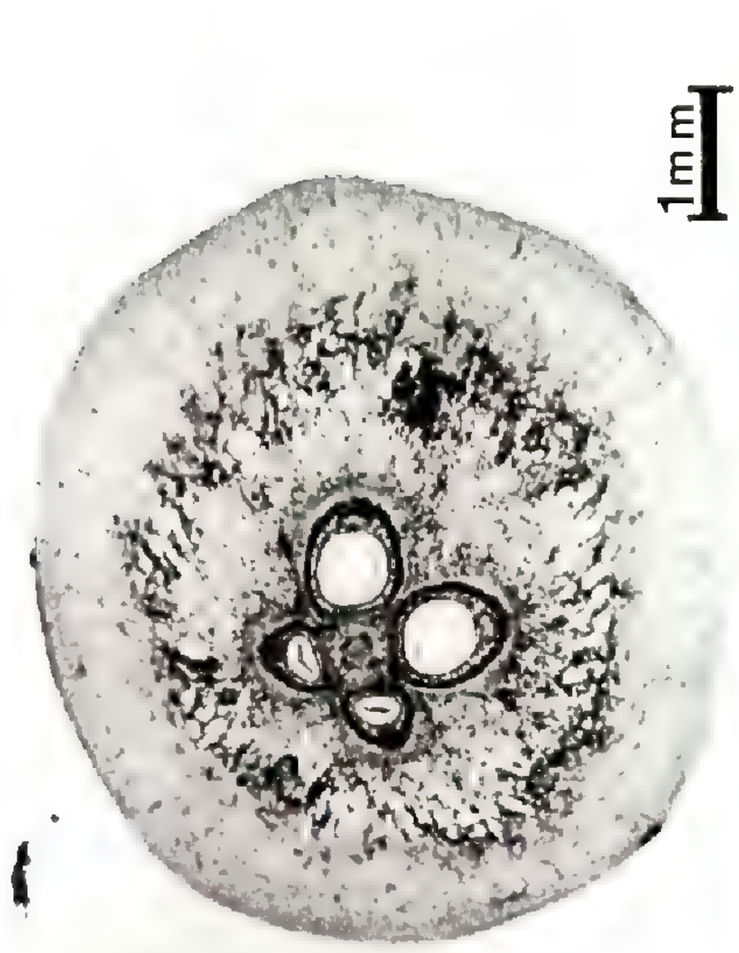
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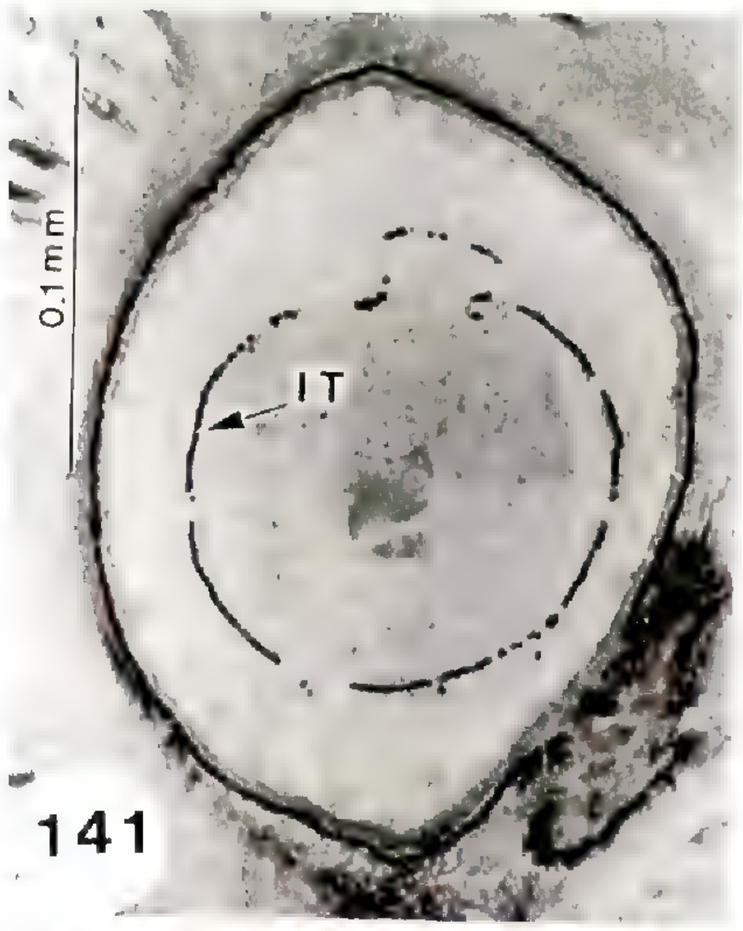
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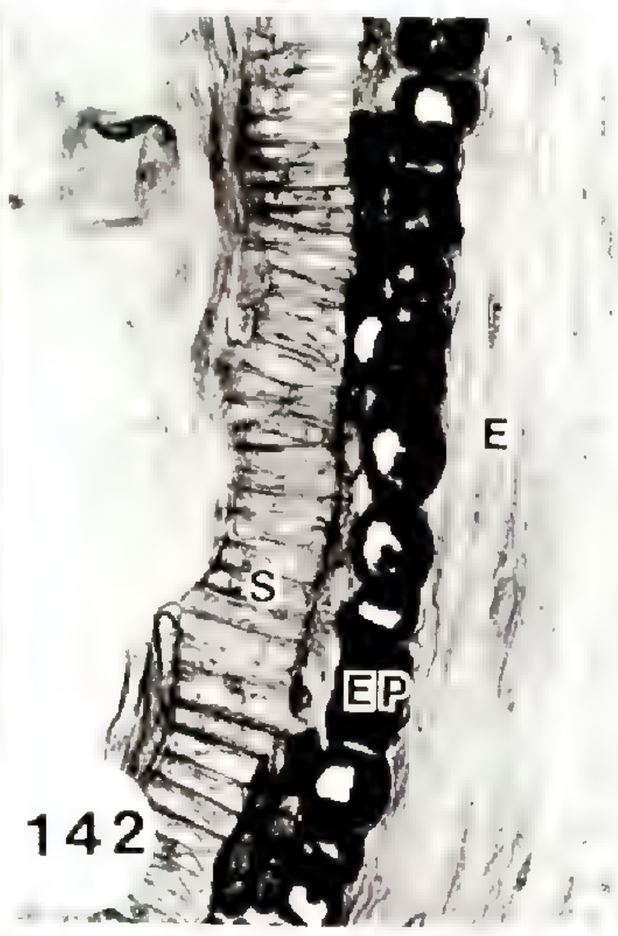
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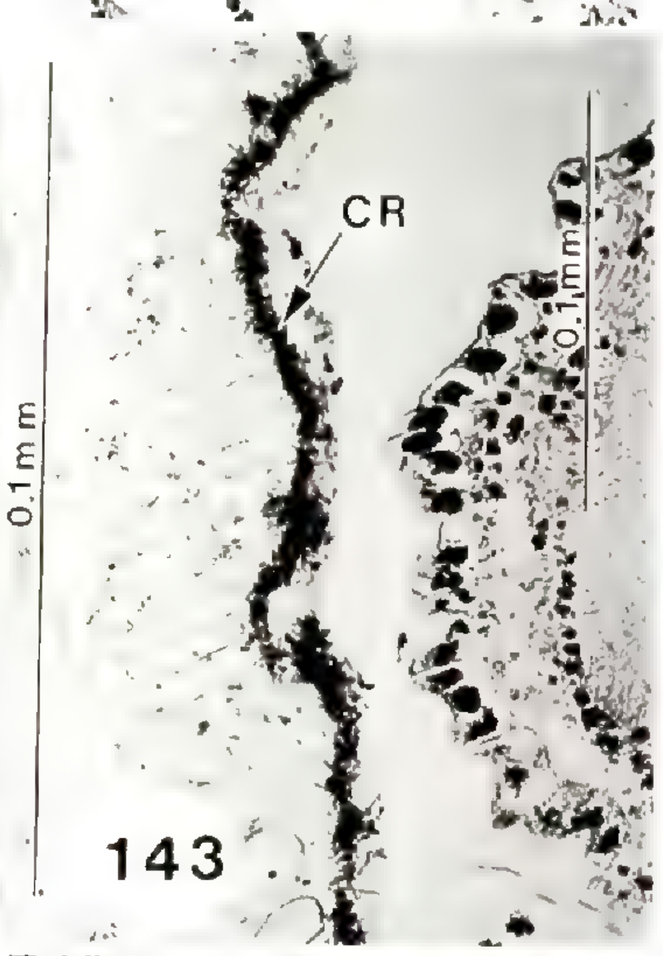
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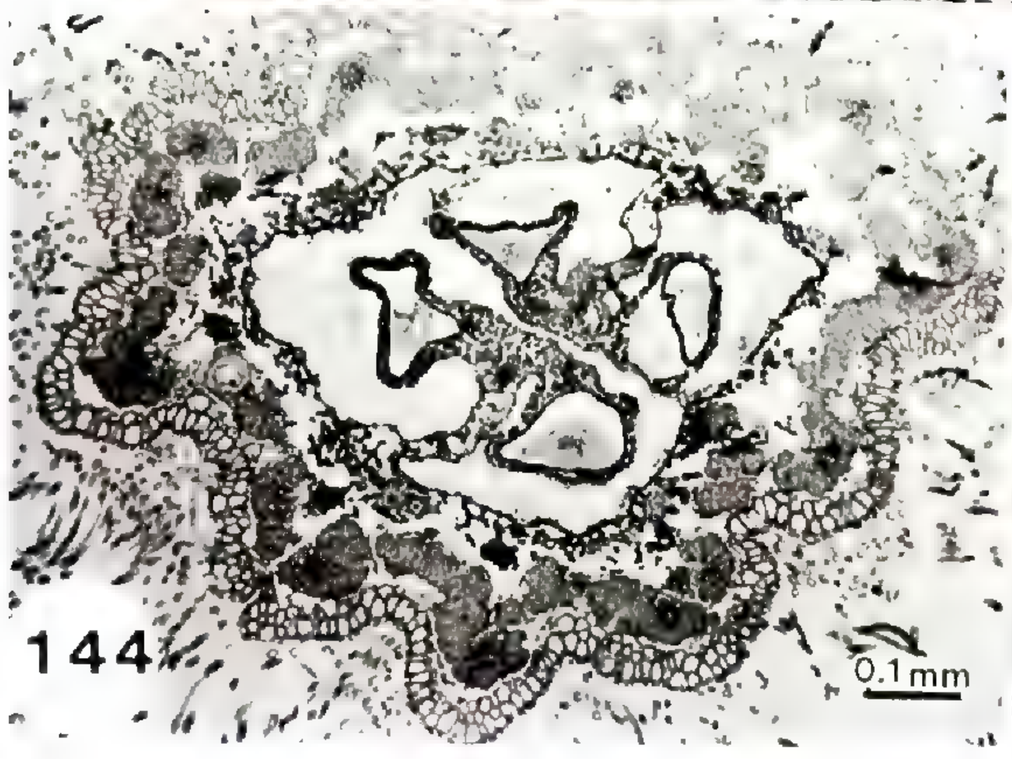
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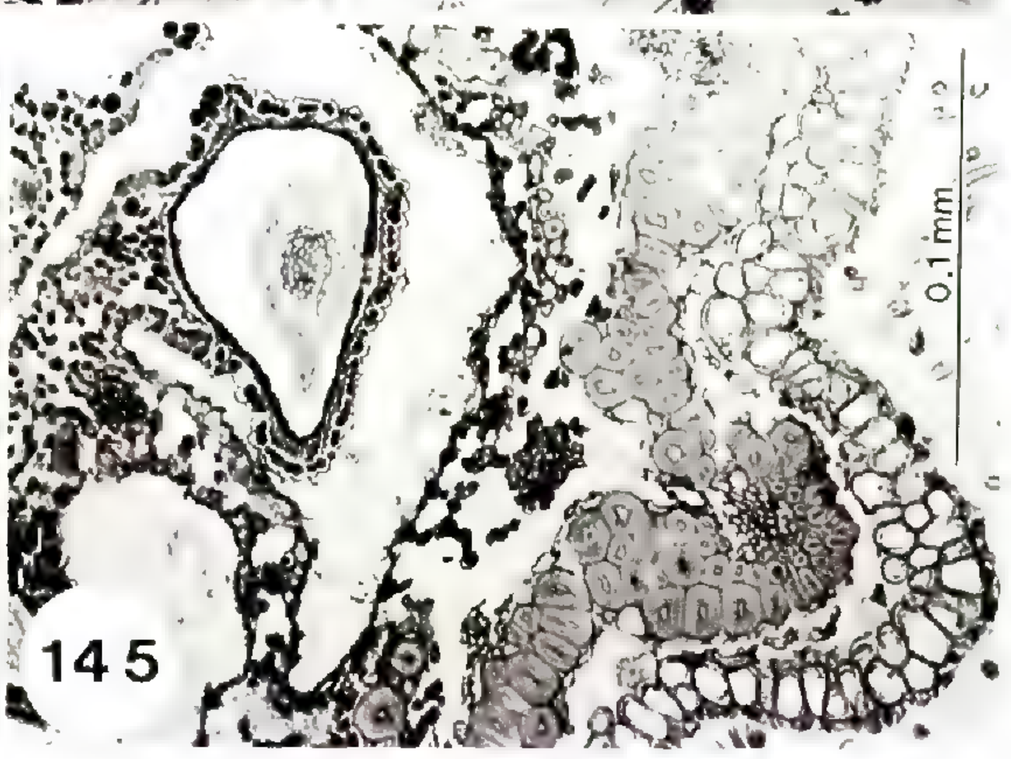
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PLATE XVI

ANATOMY OF THE PALM RHAPIS EXCELSA, X. DIFFERENTIATION OF STEM CONDUCTING TISSUE

P. B. TOMLINSON AND J. R. VINCENT

DESPITE THE APPARENT VASCULAR COMPLEXITY of the palm, its vascular development, structure, and function can be perceived quite readily. Compared with branched trees, it is architecturally simple (Hallé *et al.*, 1978). Metaxylem and protoxylem are structurally and topographically very distinct. Vascular tissues are radially as well as tangentially separated (unlike those of dicotyledons), and due to the relatively massive meristematic region and the long time course of differentiation, successive events are widely separated in time as well as in space. Finally, primary structures are not obscured by later development of secondary vascular tissues. In dicotyledons recent advances in our understanding of vascular developmental processes have required very precise analyses of serial thin sections, as in the work of Larson (1982; and earlier papers cited therein) on *Populus*.

In this paper we consider the sequence of initiation of xylem and phloem within the procambial template and the changes within these tissues as both radial and axial extension take place. Special attention is given to xylem differentiation in traces to a given leaf at various stages of its development, a topic being investigated physiologically by John Sperry at Harvard Forest.

In the first paper in this series (Zimmermann & Tomlinson, 1965), a cinematographic method of analysis was used to describe the course of vascular bundles in the mature aerial stem of the small palm *Rhapis excelsa* (Thunb.) Henry. In a topographic sense, traces serving a given leaf (leaf traces) usually branch to give an axial bundle that becomes a leaf trace at a higher level. Axial bundles in the region of leaf-trace departure are connected by short bridge bundles. In addition to establishing the principle of vascular continuity in the stem, that paper demonstrated the changes that take place in individual mature bundles throughout their length. It provided a basic, general framework (since termed the "*Rhapis*-principle"—see Zimmermann & Tomlinson, 1972; Tomlinson, 1983) for understanding the vasculature of monocotyledonous stems, which may be described as a regular pattern of outgoing leaf traces branching to generate topographically axial bundles and other derivatives. To add to the topographic analysis, in the fourth paper of the series (Zimmermann & Tomlinson, 1967), the sequence of initiation of strands within the developing crown was analyzed in terms of their inception as procambial strands. The principle of vascular development that has been shown to be generally applicable to monocotyledons was demonstrated. Procambial strands that connect to young leaf primordia are initiated within a cap of meristematic tissue. They are

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continuous with an existing leaf trace but are at first uncommitted in a distal direction to a specific future leaf primordium. These processes are difficult to visualize in static diagrams but are shown clearly in recently produced demonstration films (Zimmermann & Mattmüller, 1982).

We believe that the basic nature of the *Rhapis* type of construction has wide relevance to an understanding of monocotyledonous vascular development (Tomlinson, 1983). Our overall objective is to present an understanding of the palm crown in terms of anatomy, development, and physiology.

METHODS

The analysis involved two successive steps (see FIGURE 1) because the developing region of the shoot (the crown) is an extended structure. First, the sequence of development of vascular tissue within individual bundles was studied at early stages of development (see FIGURE 3). In this phase radial expansion predominates. Second, a less-detailed analysis was carried out of late stages of development; dye-infusion techniques were used and unembedded material of long apical portions was sectioned (see FIGURE 4). In this phase longitudinal expansion predominates. Although technically necessary, such separation into phases is artificial since growth is a continuous process.

The first method provides information about the development of the vascular connection, via protoxylem, between stems and young leaves until initiation of predominant axial extension of the internode below a leaf with an expanded blade. This initial analysis can be done with stem pieces (including the shoot apex) up to a length of about 1.5 cm (FIGURE 1, A). The second method gives information about the establishment of connection between the leaf and the metaxylem of the stem during the period when the leaf blade is fully expanded but the intercalary extension of the leaf sheath is still incomplete (FIGURE 1, B). Final maturation of metaxylem occurs as soon as internodal extension is complete. Again, separation into phases of development is artificial because growth is continuous, but it is important to appreciate that blade expansion precedes maturation of the leaf sheath and its associated internode. The "first fully mature leaf" is therefore the first leaf in which extension of all these regions is complete.

The stage at which a given developmental event occurs varies by as much as three plastochrones, depending upon the size of the crown. A leaf usually first becomes visible externally somewhere between plastochrones P8 and P11 (P1 is the first microscopically visible leaf primordium). Internodal extension is generally complete somewhere between P14 and P17. For purposes of describing the position of leaves that are only visible externally, the youngest visible leaf may be referred to as leaf 1, the next youngest as leaf 2, etc. Without dissection the numbering of such leaves by the plastochrone (P) system cannot be done. In the crown analyzed we recognized about seven leaf primordia enclosed within the apical bud and not visible externally (as in FIGURE 5, where the position of P8 corresponds to the "spear leaf"—i.e., the first externally visible leaf in the crown, its blade still unexpanded).

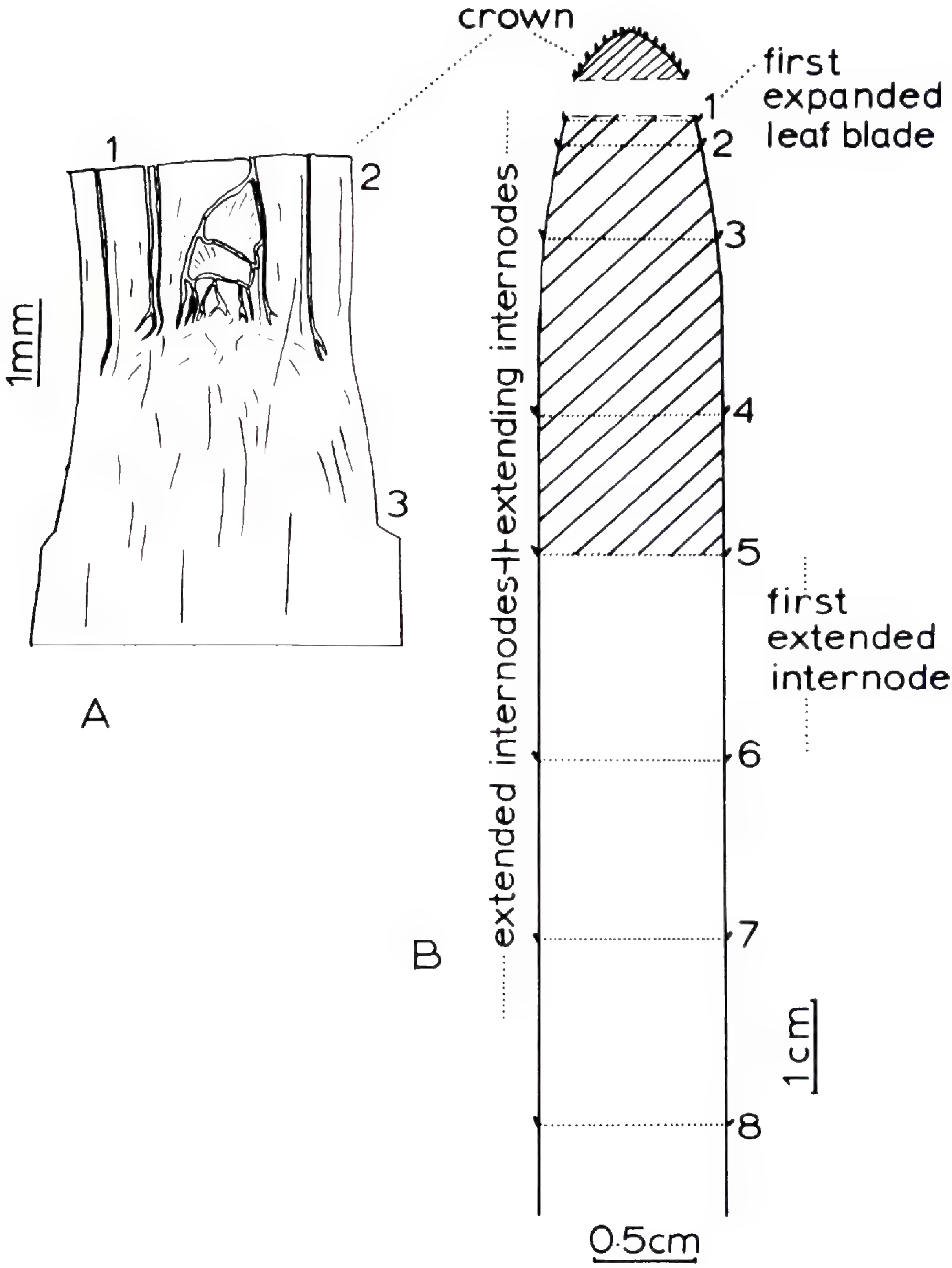

FIGURE 1. *Rhapis excelsa*, diagrams showing size of specimens used to analyze vascular development in shoot (2 methods): A, camera lucida drawing of median longitudinal section of apex about same size as that used in analytical plots (see FIGURE 5); B, diagram of axis used in experimental dye injection of single leaf, foreshortened 50%. Numbers refer approximately to corresponding expanded leaves in visible crown.

PLOTTING OF EARLY STAGES

To plot the early stages of vascular bundles, we examined three section series, including one described in a previous paper (Zimmermann & Tomlinson, 1967). These series were derived from apices from which all but the youngest enclosed leaves were trimmed. They were fixed, embedded, sectioned at 8–15 μm, stained in safranin and Delafield's haematoxylin, and mounted in the usual way, but with only a single section on each slide. Plotting was carried out by the drawing and shuttle methods of Zimmermann and Tomlinson (1966)—i.e., either with a drawing attachment to a Wild M-20 microscope or with two separate microscopes connected by an optical bridge. These methods provided precise alignment for successive sections. Single major leaf traces belonging to successively older leaves were followed, starting with P1 (the youngest leaf primordium), in a basipetal direction from the level of insertion of the leaf. In *Rhapis* the crown is a shallow cone (FIGURE 1, A; see also Zimmermann & Tomlinson, 1967, *fig. 4*), so it is possible to follow traces continuously in one direction. Positions of each trace measured at regular intervals were plotted on graph paper, with only the radial coordinate considered, the helical or tangential displacement being ignored for diagrammatic purposes (see Zimmermann & Tomlinson, 1967, *fig. 2*).

At each plotted level the number of differentiated xylem elements was counted. To facilitate recognition of differentiated protoxylem elements, transverse sections were viewed through partly crossed polarizing filters; the birefringence of cell walls of fully mature elements rendered them conspicuous. It was considerably more difficult to recognize protophloem elements at very early stages of vascular differentiation in bundles that were cut somewhat obliquely. The criteria that we used were presence of cell walls densely stained with haematoxylin, and cell contents relatively unstained or even clear. Sometimes simple sieve plates could be seen in face view, making the identification of sieve elements unequivocal. The principal objective was to establish whether or not phloem was continuously acropetal in its differentiation.

GENERAL ANALYSIS OF LATE STAGES

To show late stages of xylem differentiation and particularly to identify the vascular contribution of a given leaf in its final stages of development, dye ascent and descent experiments were conducted using Schiff's reagent (reduced-acid fuchsin) after a preliminary perfusion with 0.5 percent periodic acid as an aldehydic mordant. This was similar to the method used by Priestley and colleagues (1935) to trace bundles from specific leaves in *Alstroemeria* with Magdala red as a marker stain but without any mordant. In the ascent experiment the stem was cut about 20 cm below the shoot apex. The cut end was immersed in dye, and suction was applied to a cut leaf. Distally, dye moved preferentially into the traces of the leaf to which suction was applied. In the more-informative descent experiments, a flask containing the dye was attached via an air-tight seal to the cut petiolar stump of a given expanded leaf of a detached shoot. Dye moved only into the traces of the injected leaf. On different shoots successive leaves from the youngest to the fifth-youngest expanded

leaves were infiltrated. The dye penetrated the shoot over a period of about 24 hours; it could then be recognized in its colored, oxidized form in the cell walls of the leaf-trace xylem continuous from the cut leaf, as seen in sections cut at successively lower levels (e.g., FIGURE 4). In this way the trace system from a given leaf could be recognized in freehand sections of the shoot at successively lower levels. Sections were dehydrated and mounted in Permount without further staining. Traces were followed to a maximum distance of 36 cm—i.e., up to about 15 internodes below the morphological level of insertion of the injected leaf. Additional sections cut at intervals from other shoots, stained in phloroglucinol and concentrated HCl, showed the general progression of late stages of maturation of lignified tracheary elements, but without reference to a particular leaf. These sections were useful for recognizing the highest level of maturation of metaxylem.

RESULTS

GENERAL FEATURES OF VASCULAR DIFFERENTIATION

EARLY STAGES (RADIAL EXPANSION PREDOMINANT). Observation of single sections gives general information about the progress of vascular differentiation at a single level. FIGURE 2 represents the appearance of a vascular bundle at an approximately comparable level in successive plastochrones, so that ontogenetic events in a single bundle are simulated. The illustrations were produced by selecting an arbitrary standard level (a major leaf trace at its most central location) and, with the aid of the drawing apparatus, making a drawing for a comparable bundle serving a leaf at successive plastochrones. ("Standard level" refers to an equivalent position below successive older leaves.) The drawings are thus illustrative of the general process of vascular differentiation at that particular level. Other sequences at other levels are shown photographically in FIGURE 3. Precise information about developmental events in different parts of representative individual bundles is included in the plots (FIGURES 5, 6).

The procambial strand is visible in transverse section as a group of narrow elements that retain a meristematic appearance in contrast to the surrounding vacuolated cells (FIGURES 2, A; 3, A). We have not been concerned in this study with the details of the appearance of procambial cells or with the method by which the diameter of the vascular strand is increased, although this is an important early process in the development of the vascular bundle (e.g., the changes within FIGURES 2, A–E, and 3, A, B). Cell divisions in later stages of procambial development are mainly longitudinal. In longitudinal section the strand comes to have a characteristic "tiger-tail" appearance because nuclei of adjacent, recently divided procambial cells lie at the same level. Cells in the center of the bundle vacuolate early, in contrast to those in the inner (xylic) and outer (phloic) regions, but cell division still continues in them and produces a temporary "cambiumlike" condition seen in transverse section (FIGURE 2, D).

At the standard level illustrated (FIGURE 2), the first appearance of vascular

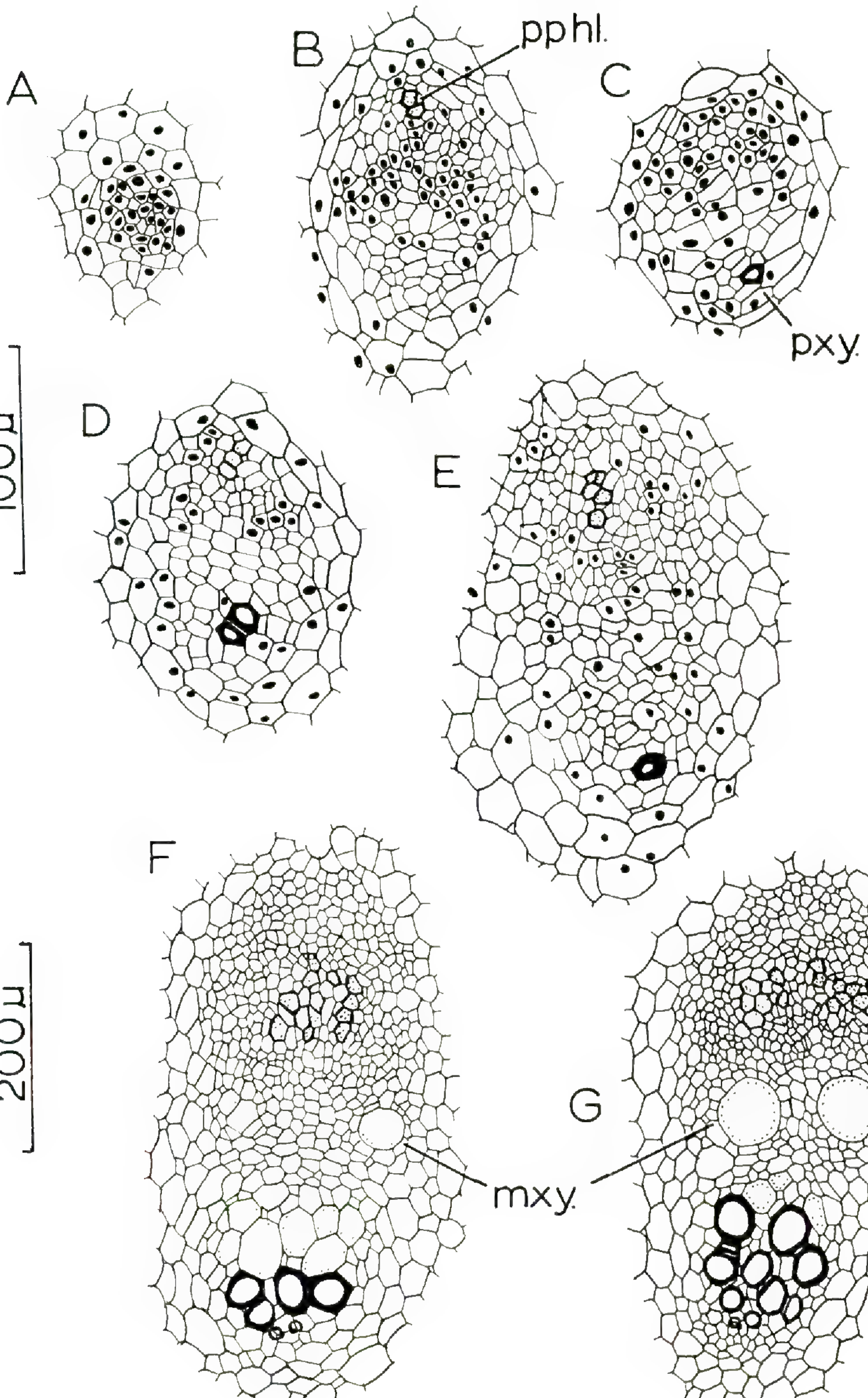

FIGURE 2. *Rhapis excelsa,* transverse sections of developing leaf traces to progressively older leaves (drawn from series used in preparing FIGURE 5). Bundles represented at different axial distances below shoot apex and estimated to serve leaf primordia (P) indicated: A, 0.45 mm (P3), no differentiated vascular tissue; B, 1 mm (P5), protophloem (pphl.) only; C, 1 mm (P5), protoxylem (pxy.) only; D, 1 mm (P6), protoxylem and protophloem; E, 1.8 mm (P7), protoxylem and protophloem; F, 2.8 mm (P9), first differentiation of metaxylem (mxy.); G, 12.8 mm (P11), differentiating metaxylem vessels

tissue is the development of protophloem toward the outside (peripherally oriented) part of the procambial strand (FIGURE 2, B). In the permanent preparations used in this analysis, differentiated protophloem sieve elements have somewhat thickened angular walls. These walls stain densely with haematoxylin, and either the protoplast stains lightly or the cell lumen appears completely empty. Simple transverse sieve plates are often evident. Protophloem elements of this kind have a diameter of about 8–10 μm. At the given level sieve-element (phloem) differentiation scarcely precedes protoxylem differentiation and in some strands even follows it (FIGURE 2, C). We found no precise evidence for discontinuous sieve-element differentiation, although in a few bundles uncertainty in recognizing phloem elements sometimes gave this impression within a few adjacent sections.

Later differentiation of sieve elements at any one level was always in a centripetal direction and involved elements somewhat wider (10–15 μm) than those first detected (FIGURE 3, B). In association with these changes, there was evidence of disruption and collapse of the youngest protophloem elements. In transverse appearance the lumen of the first-formed sieve elements becomes irregular and is finally occluded by expansion of surrounding cells. In still later stages the position of the protophloem is marked by a densely stained region of cell-wall material. In the axial portion of a mature bundle, the protophloem region is obscure and included within the innermost bundle-sheath fibers. It proved difficult in the kind of sections used to quantify (in terms of numbers of functional sieve tubes) the sequence of events involved in early phloem differentiation because of the problems of recognizing both early stages of sieve-element differentiation and their later collapse.

In transverse sections of young leaf traces, protoxylem can first be recognized unequivocally as enlarged cells (ca. 10–15 μm diameter) with thick, lignified walls that stain with safranin (FIGURE 2, C, D). Polarizing optics confirmed the existence of a thickened birefringent cell wall. In addition the cell lumen always appears empty. The first protoxylem element occurs on the inner side of the procambial strand, remote from the protophloem, and is followed by a succession of elements that appear in centrifugal order. Later-formed elements are somewhat wider and more conspicuous; they form a circular or wedge-shaped group of cells in transverse section (FIGURE 2, G). The intervening area between protoxylem and protophloem is occupied by procambial cells, and differentiation within this region varies depending on the level at which one examines a given strand, as is indicated later (FIGURE 3, C, D). The distance between first-formed xylem and phloem elements actually increases as the bundle matures, due to the increase in number of procambial cells by the continued longitudinal divisions already mentioned.

We have not followed developmental changes in detail in longitudinal sec-

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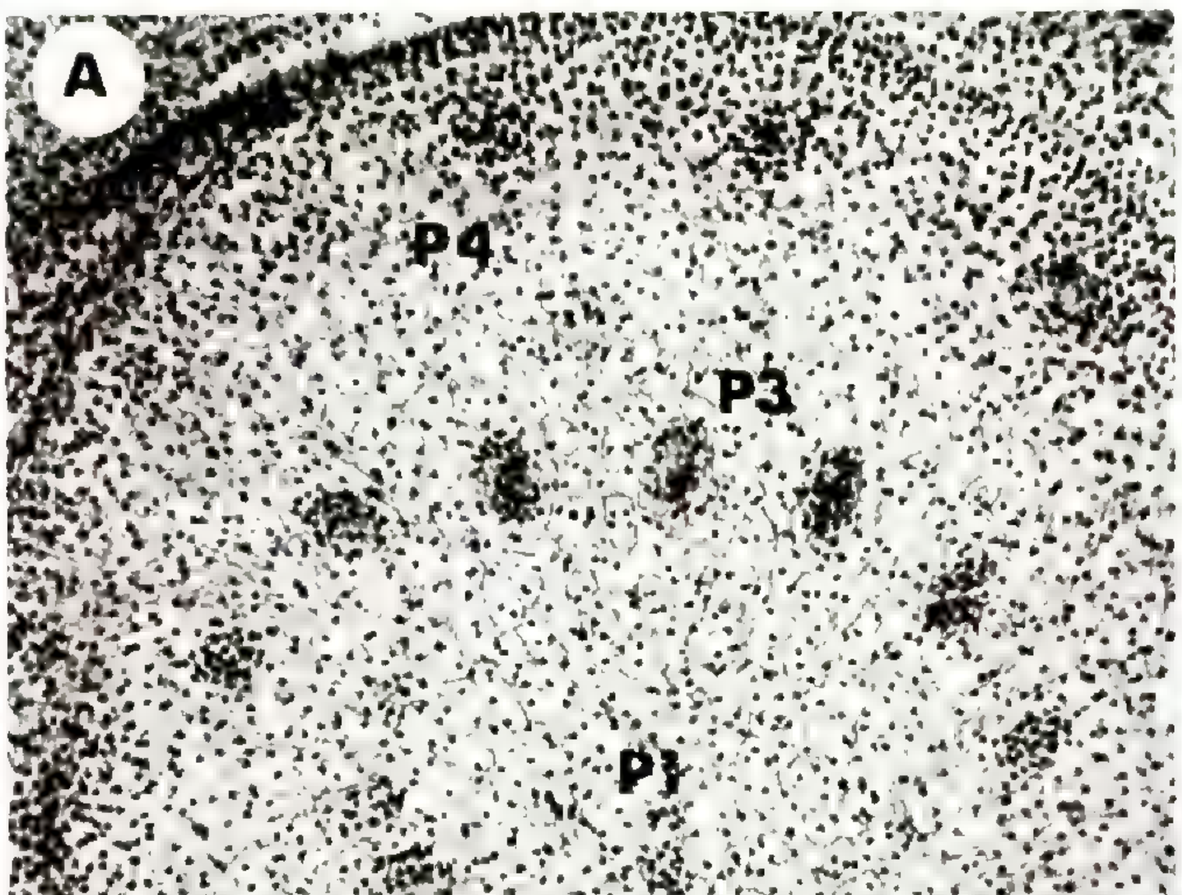
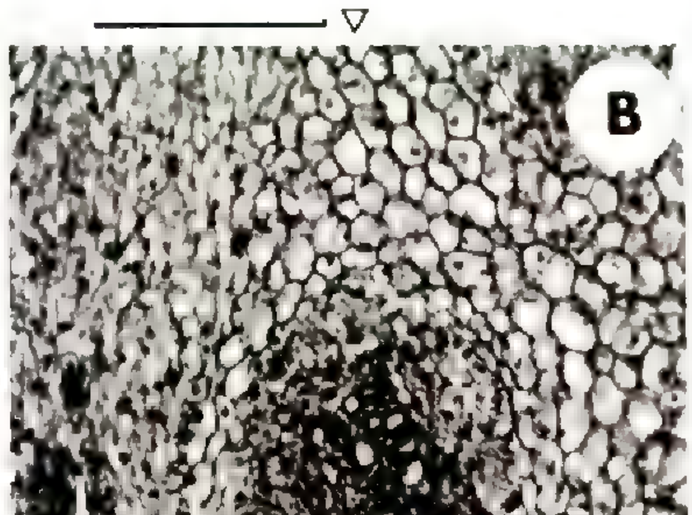
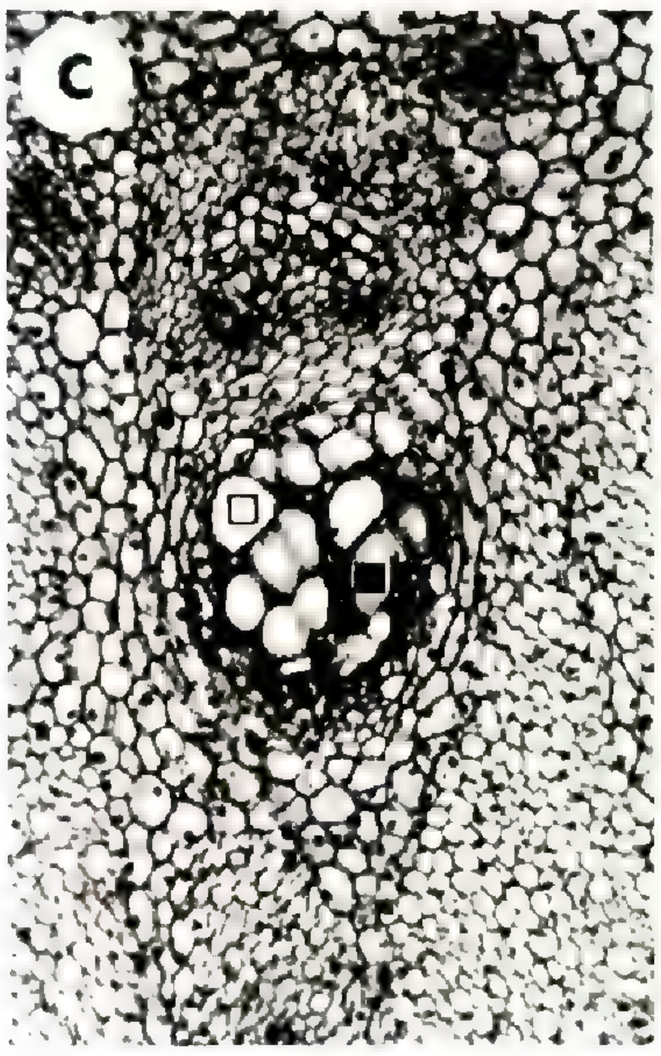
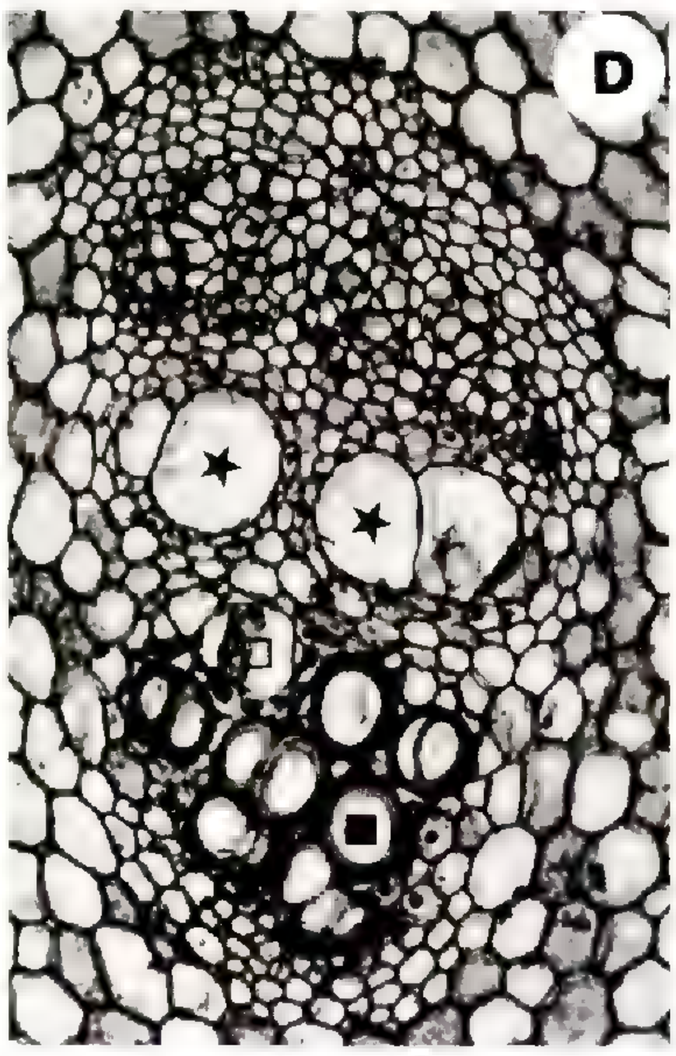
near maximum diameter. (Black circles = nuclei, stippled areas = sieve tubes of protophloem, solid black walls = protoxylem, lumen outline dotted = differentiating protoxylem and metaxylem elements.)









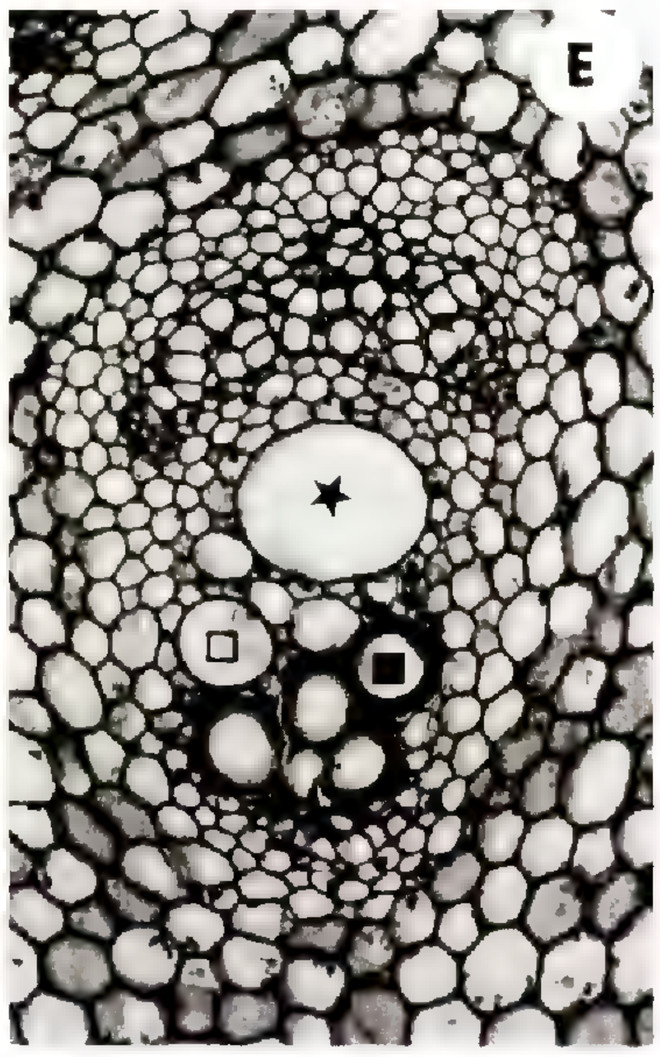


FIGURE 3. *Rhapis excelsa,* photomicrographs of 15-μm-thick transverse sections from paraffin-embedded material. A, 0.3 mm below shoot apex: leaf-trace system to P1, P2, and P3 still discretely recognizable within stem, trace system to P4 within leaf base. B, 1.8 mm below shoot apex: major leaf trace to P8; protoxylem and protophloem well developed, early metaxylem differentiation evident. C, 5.7 mm below shoot apex: major leaf trace to P10 close to periphery of central cylinder; protoxylem and protophloem still incompletely differentiated (no metaxylem in this part of leaf trace). D, 15 mm below shoot apex: major leaf trace; protoxylem almost completely differentiated, metaxylem elements not in contact with protoxylem almost completely expanded but still thin walled. E, 13.8 mm below shoot apex: axial bundle; single incompletely differentiated metaxylem

tions. Serial sections show that the protoxylem elements are short, but with annular or helical wall thickenings, and are thus presumably extensible. Protophloem elements are also short.

At the standard level illustrated in FIGURE 2, metaxylem differentiation begins at a very early stage when there is little mature protoxylem (see FIGURE 3, B). In transverse view the first evidence for metaxylem differentiation is the enlargement and vacuolation of a pair of cells toward the middle of the bundle but laterally widely separated from each other (FIGURE 2, F). These initials subsequently widen considerably and block out the characteristic metaxylem pattern. The walls of the enlarging vacuolating cells remain unthickened and contrast with the lignified, thick, birefringent walls of the protoxylem (FIGURE 2, G). Maturation of metaxylem occurs very late, well below the crown, and only in bundles that are directly in association with older expanded leaves and that run through fully extended internodes (i.e., in the unshaded part of FIGURE 1, B), as is described later.

Depending on the level examined, protoxylem may or may not be in direct lateral contact with the metaxylem (cf. FIGURE 3, D and E); in the distal part of any axial bundle, at the level of its divergence toward a leaf, protoxylem is separated from metaxylem by a broad region of procambial cells that mostly mature as parenchyma cells. In late stages of differentiation, the cells of this conjunctive parenchyma become somewhat radially seriated (FIGURE 2, D), indicative of further late, regular tangential division, which is completed before metaxylem differentiation begins. Evidence for the time and regularity of division is provided by the identical length and the coincident end walls, at any one level, of the wide vessel elements and the metaphloem sieve tubes (Parthasarathy & Tomlinson, 1967). However, the situation is complicated by the late differentiation of tracheary elements on the outer face of the protoxylem, as is described later.

Fiber differentiation outside the protophloem is initiated early but is long continued. Maturation of fibers begins in the region of the protophloem, but the pattern within the future fibrous sheath of the vascular bundle becomes complex. The extent of apical intrusive growth of differentiating fibers is not known. However, in larger palms there are regular trends of change of fiber length throughout single stems, indicating a high degree of endogenous control of fiber length but some correlation with internode length (Tomlinson & Zimmermann, 1967).

LATE CHANGES (INTERNODAL EXTENSION PREDOMINANT). In any one leaf trace followed basipetally, the gap between protoxylem and metaxylem decreases, and at some level incompletely differentiated protoxylem elements are seen to be contiguous with incompletely differentiated metaxylem elements (FIGURE 3, E). Fully differentiated contiguous protoxylem and metaxylem elements

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vessel contiguous with incompletely differentiated (presumed) protoxylem elements. (Empty squares = differentiating protoxylem, solid squares = mature protoxylem, solid stars = differentiating metaxylem. Scale for A = 50 μm, for B–E = 100 μm.)

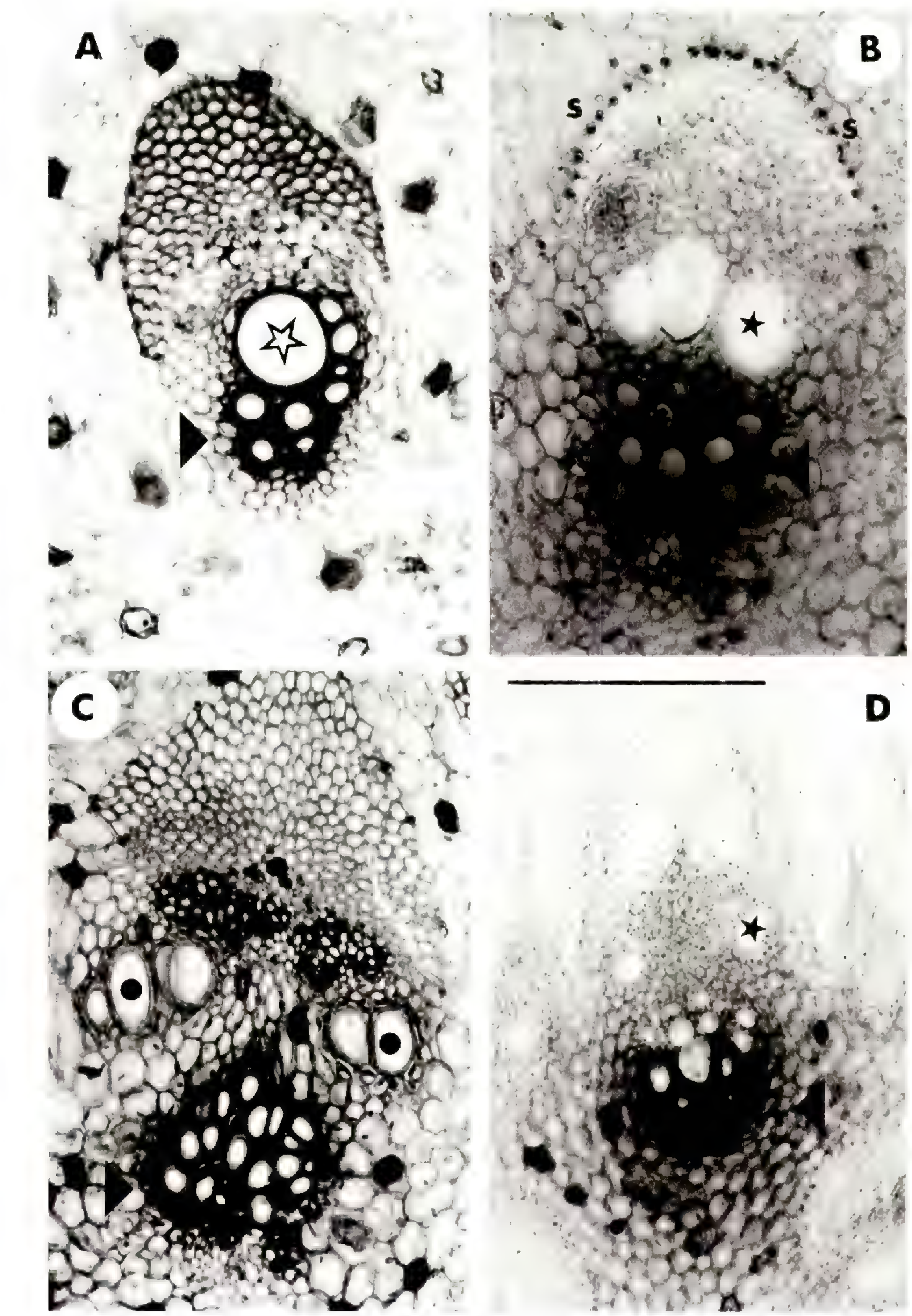

FIGURE 4. *Rhapis excelsa,* transverse sections about 50 μm thick from fresh, unembedded material after dye-descent injection experiments. Dark staining indicates presence of Schiff's reagent in xylem. A, major leaf trace to first fully expanded leaf 3.9 cm below its morphological insertion: protoxylem and metaxylem fully differentiated and closely contiguous so dye moves from former to latter (downward in this experiment). B, major leaf trace to second fully expanded leaf 3 cm below its morphological insertion: protoxylem fully differentiated and conducts dye readily downward; metaxylem incompletely differentiated and not contiguous with protoxylem so dye not conducted. C, major

occur only in internodes in which extension is complete (FIGURE 4, A). Transport of water is then possible between the two types of element, as the dye descent and ascent experiments show. In axial bundles a single metaxylem element is differentiated in the absence of any protoxylem. This construction also applies to bridge bundles (and presumably to branch traces, although we have not examined their development in detail).

The peripheral part of each bundle differentiates as the fibrous cap, the extent of which is directly related to the proximity of the bundle to the stem center: peripheral bundles develop a wide fibrous sheath, central bundles a narrow one. Stegmata (silica cells) are conspicuous in early stages of maturation of the fibers (e.g., s in FIGURE 4, B).

Although we have not followed individual bundles directly over long distances, the overall maturation of conducting elements can be seen in sections at progressively lower levels. In developmental terms there is thus an advancing "front" of maturation so that overall vascular differentiation is at about the same level of advancement in all bundles.

VASCULAR DIFFERENTIATION IN THREE DIMENSIONS

Changes in vascular pattern with bundle position and age may first be examined from plots of major bundles to leaves at successive plastochrone intervals. These positions are plotted collectively in FIGURE 5, with details of the apical region enlarged in FIGURE 6. We should emphasize that quantitative information relates to the one crown from which the plot was made. Different crowns give different absolute values, but the relative values are much the same. The differences (largely quantitative) between intermediate and minor bundles are explained later.

This reductionist approach demonstrates the basic pattern for all bundles, but is free of the topographic complexity occurring in the crown due to the large number of bundles involved. It should be reemphasized that, according to the earlier study of Zimmermann and Tomlinson (1967), differentiation of the axial bundle is continuously acropetal in relation to the meristematic cap just below the shoot apex. Evidence that some vascular tissue develops in a continuous acropetal direction comes from the observation that undifferentiated vascular tissue is continuous below with differentiating and ultimately

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leaf trace to fifth fully expanded leaf 2 cm below its morphological insertion: protoxylem and metaxylem both fully mature but only protoxylem conducts dye downward; metaxylem not contiguous with protoxylem at this level and remains unstained. D, major leaf trace to first fully expanded leaf 0.8 cm below its morphological insertion: only differentiated protoxylem (dark stained) conducts dye downward; undifferentiated protoxylem and metaxylem remain unstained (compare A, showing comparable bundle at lower level; hydraulic constriction apparent). (Open star = mature metaxylem vessel contiguous with protoxylem; solid triangles = protoxylem with densely stained walls; solid circles = metaxylem not in contact with protoxylem, unstained in this experiment; solid stars = differentiating and nonconducting metaxylem; S = stegmata. Scale bar = 200 μm.)

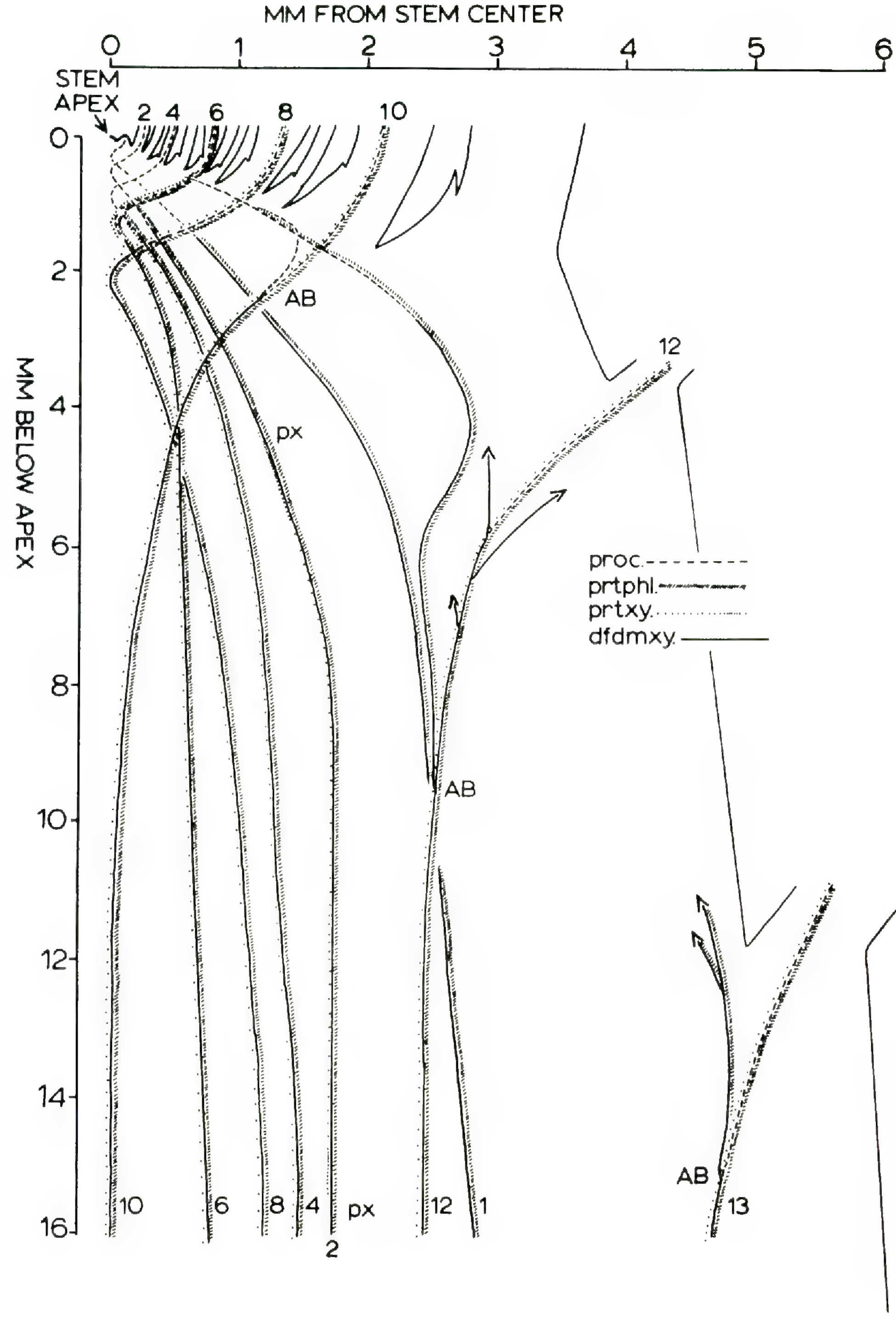

FIGURE 5. *Rhapis excelsa:* schematic longitudinal view of distribution of differentiating vascular tissues within major bundles to several successive leaves in developing crown, from same series used to produce FIGURE 2 (see FIGURE 6 for apical details). Axial dimension foreshortened about 50%. All leaves shown as if occupying single orthostichy instead of actual 2/5 spiral phyllotaxy; internal helical course of vascular bundles also ignored. Irregular width of leaf bases an artifact of plotting and display.

mature vascular tissue. These statements apply to protophloem and metaxylem, which are continuous acropetally. However, protoxylem is discontinuous and differentiates bidirectionally.

PROTOPHLOEM DIFFERENTIATION. Within the median leaf trace to P1, protophloem is not recognizable until nearly 1 mm below the shoot apex has been traversed (FIGURE 6). This is true of median major traces to the next four older leaf primordia (P2–P5). The precise level is somewhat uncertain because it is not easy to detect the first-formed protophloem element. Once located, however, protophloem can be traced continuously in a basipetal direction in the axial bundle. From sections of older vascular bundles, it seems that the differentiation of phloem, once initiated, is continuous at any one level, with new elements added in a centripetal direction (FIGURE 2, D–G). The distinction between elements differentiated during (protophloem) and after (metaphloem) elongation of the vascular procambium is somewhat arbitrary, but can be inferred indirectly by considering the level at which metaxylem first matures (which indicates cessation of organ extension). We have not investigated structural differences between protophloem and metaphloem established by this indirect method.

Protophloem continuity into a leaf is first evident in a trace to P6 and is then found in major traces to all older leaves (FIGURE 5).

PROTOXYLEM DIFFERENTIATION. Protoxylem was not detected at any level in a major trace to the youngest leaf primordium (P1) within the sectioned series. It can be seen in a trace to P2, but only at a considerable distance below the shoot apex—about 4 mm in an axial direction (FIGURE 5, upper px). Traced further in a basipetal direction, this protoxylem disappears at a level about 16 mm below the shoot apex (FIGURE 5, lower px). This is the developmental origin for the basipetal discontinuity of the protoxylem, evident in the mature stem. Since within a single plastochrone (P1 to P2) protoxylem appears and becomes elaborated over a distance of 12 mm, its differentiation is obviously very rapid. Further extension of this distance until protoxylem is continuous into the leaf base does not occur until the leaf is in position P6. In this leaf there is initially a short discontinuity within the leaf base (between px and px in FIGURE 6) representing the level of the intercalary leaf meristem; protoxylem can be seen in the leaf base above this level of discontinuity in the bundle investigated. Protoxylem continuity between leaf and stem is established in P7

Single major trace plotted to P1, 2, 4, 6, 8, 10, 12, and 13. In this crown P8 is youngest externally visible leaf ("spear leaf"); P9, first fully expanded leaf; P14 or P15 (outside this view), youngest leaf inserted above fully extended (mature) internode (see FIGURE 1). (Dashed lines = procambium (proc.), with or without differentiated vascular tissues; hatched lines = mature protophloem (prtphl.); dotted lines = mature protoxylem (prtxy.); solid lines = vascular bundle with differentiated (but still immature) metaxylem (dfdmxy.); AB = level of departure of axial bundle from leaf trace; px (above and below) = upper and lower limits of differentiated protoxylem in axial portion of major leaf trace to P2; arrows = bundles diverging from outgoing leaf trace with further extremity not plotted.)

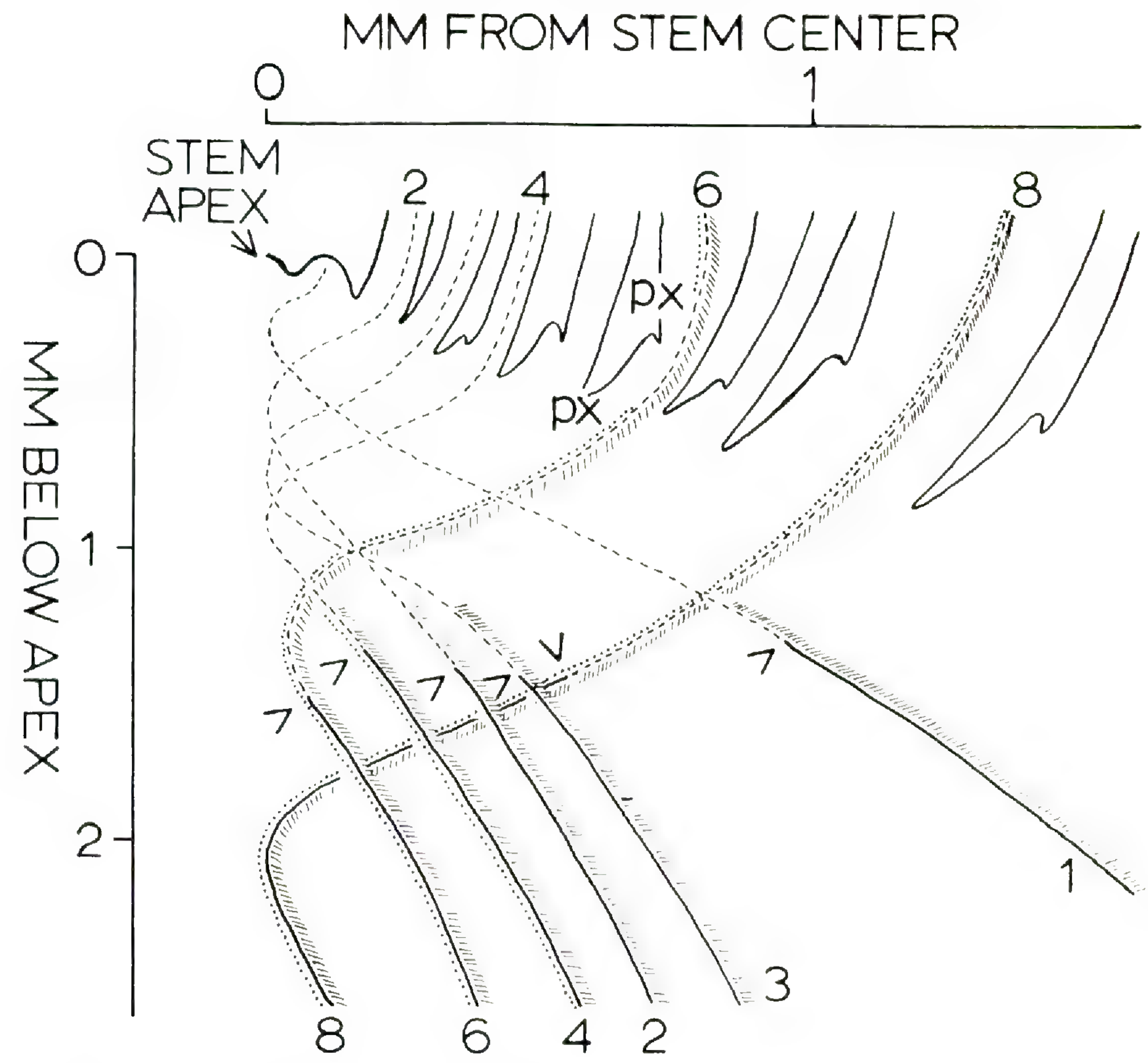

FIGURE 6. *Rhapis excelsa,* enlargement of crown region of FIGURE 5 to show early stages of vascular differentiation in major leaf trace to P1, 2, 4, 6, and 8. (Arrowheads = most distal level at which metaxylem differentiation first detected; discontinuity px to px in trace to P6 = discontinuity of mature protoxylem in leaf base. Shading conventions as for FIGURE 5.)

(not plotted in FIGURES 5 and 6) but is represented within the vascular bundle only by a single file of protoxylem elements at the leaf base. All older leaves (e.g., P8 in FIGURE 6) include protoxylem continuous from stem to leaf and in several overlapping files. This information demonstrates the intrinsic discontinuity of protoxylem. From the change in topography of a given bundle as a result of combined radial and axial displacement, it is reasonable to describe the further overall course of protoxylem differentiation as "bidirectional."

At any one level the amount of protoxylem progressively increases because differentiation of new elements proceeds faster than old elements are obliterated (cf. FIGURES 2, A and B; 3, B and C). Because of the protoxylem discontinuity, there is a basal decline in number of protoxylem elements that can be interpreted as evidence of the basipetal component of bidirectional differentiation. FIGURE 7, a plot of the total number of elements in all vascular bundles in the

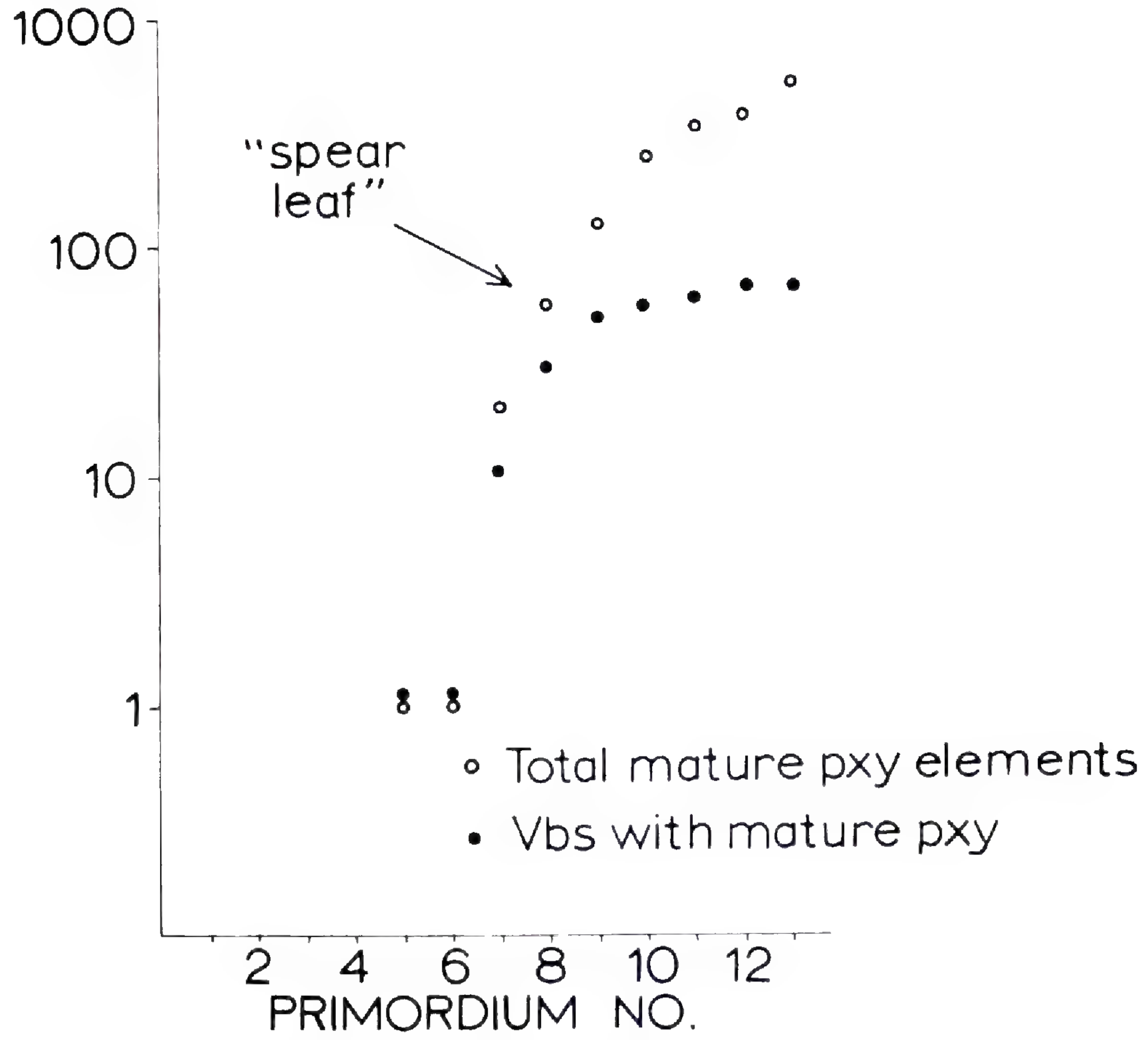

FIGURE 7. *Rhapis excelsa*, protoxylem development at leaf insertion of successively older leaves. (Closed circles = number of vascular bundles in leaf bases of successive primordia (P1 is youngest microscopically visible primordium); open circles = total mature protoxylem elements at same level.) P9 is first leaf with fully expanded blade; protoxylem maturation continues in leaf base for at least 4 plastochrones after leaf blade has expanded.

base of each leaf at successive plastochrones, indicates the extent of protoxylem connection of successive leaves but underestimates (because of protoxylem obliteration) total protoxylem produced. The information is sufficient to show that P8, the "spear leaf," is the first leaf with appreciable xylem contact with the stem, but that later leaves add considerably to their xylem transport capacity without adding new vascular bundles. This diagram can be compared with *fig. 4* in Zimmermann and Tomlinson (1967), which shows the total of all vascular bundles in successively older leaves.

METAXYLEM DIFFERENTIATION. Two stages of metaxylem differentiation can be recognized: early, when the conspicuous metaxylem vessels are first initiated (e.g., FIGURES 2, 3, 6); and late, when the cell contents are lost and wall thickening is completed (unshaded portion of FIGURE 1). In the mature vascular bundle at distal levels close to the level of branching as a leaf trace (e.g., lower

AB in FIGURE 5), the conspicuous metaxylem is represented by either a single vessel or a widely separated pair of vessels. Overlapping ends of vessels are commonly seen, especially in the region of attachment of bridges and branch traces (e.g., left-hand group of vessels in FIGURE 2, F). At any level where metaxylem is present, the elements are first visible as cells that vacuolate and enlarge conspicuously, in contrast to adjacent cells, most of which mature as narrow conjunctive parenchyma cells. This contrast occurs, for example, in a major trace to P1 at an axial distance of about 1.5 mm below the shoot apex (FIGURE 5). Significantly, this is well before protoxylem is differentiated in the same strand at this level. Protoxylem in the leaf trace does not occur much in advance of the differentiating metaxylem until about the time when the associated leaf is in position P5. After this, protoxylem is always continuous into the leaf base, as we have established. Metaxylem does not differentiate into the outgoing leaf trace but is continuous axially via bridges to adjacent axial bundles. These axial bundles themselves become recognizable as procambial strands in the crown just below the meristematic cap (Zimmermann & Tomlinson, 1966). However, bridges with early stages of metaxylem differentiation do not become recognizable until about the level of insertion of P12—i.e., almost 5 mm below the shoot apex proper in an axial direction. Such a leaf is the fourth-youngest fully expanded leaf in the crown illustrated in FIGURE 5. The relatively rapid advance of metaxylem differentiation within an axial bundle can be seen by comparing the procambial strand diverging from the leaf trace to P10 at the upper AB with that diverging to P12 at the middle AB in FIGURE 5.

Late stages of metaxylem maturation involve development of secondary wall layers and their lignification, together with loss of cell contents. Examination of free-hand sections stained with phloroglucinol and concentrated HCl shows lignified walls in wide metaxylem vessels at linear distances of about 3–4 cm below the shoot apex. This is about the level of insertion of the fifth leaf below the first fully expanded leaf and is always at the level where internode elongation has just ceased (FIGURE 1, B, unhatched portion). Maturation of metaxylem appears to be continuously acropetal.

In addition to the wide metaxylem, there are late-differentiated tracheary elements on the outer surface of the protoxylem strand that may not be totally mature until the internode (and therefore the vascular bundle) is completely extended (FIGURE 3, D, E, open squares). This becomes obvious when late stages of vascular differentiation are examined, but it was not considered when the mature structure was described. Consequently, it was assumed that all narrow elements on the inner face of the leaf trace were protoxylem tracheids (Zimmermann & Tomlinson, 1965). The late-maturing elements in this position, however, must be metaxylem, and they possibly correspond to some of the narrow vessel elements observed by Zimmermann and Sperry (1983) in macerated material from stems. They occupy only a limited part of the leaf trace since they occur just below the level where the protoxylem first diverges from the metaxylem within a given bundle. However, they are functionally important because this is the region in which interchange of water between metaxylem and protoxylem occurs (FIGURE 4, A).

Establishment of the Vascular Connection

The level at which the "descending" protoxylem of the leaf trace becomes contiguous with the "ascending" mature metaxylem can be determined from dye descent experiments, since the downward-moving dye initially descends in the protoxylem and can only enter the metaxylem of the axial bundle when a) this is mature, and b) the two tissues are in direct contact (Figure 4). Because the dye is initially restricted to the traces connecting the injected leaf to the stem, the vascular supply to that leaf can be identified in the stem. The juxtaposition of the two types of xylem can also be readily recognized in sections.

Movement of dye from protoxylem to axial metaxylem occurs (see Figure 4, A) in the trace system of leaf P9 and can be observed in the internode below P13 or P14—i.e., the internode in which extension has just been completed. (This association is, of course, rational and a simple consequence of the definition of metaxylem, which cannot mature completely within an extending organ.) The area of overlap (vascular insertion) is also mature at this level. At a higher level in the same bundle, only protoxylem is fully mature and conducts the dye; metaxylem is still undifferentiated (see Figure 4, B) and cannot transmit the dye even if it is contiguous with the mature protoxylem. The same considerations apply when protoxylem and metaxylem are not contiguous, regardless of whether metaxylem is mature (see Figure 4, C) or not (see Figure 4, D).

Maturation of Intermediate and Minor Bundles

Each leaf is supplied with about 100 vascular leaf traces that connect with the central cylinder of the stem. These have been termed major, intermediate, and minor bundles according to their topographic arrangement and time of appearance in the leaf base (Zimmermann & Tomlinson, 1965). Major bundles appear earliest and diverge from the stem center; intermediate ones appear later and diverge from a position nearer the stem periphery; and minor ones appear last and are restricted entirely to the periphery of the central cylinder. These designations are arbitrary since there is a developmental continuum (Zimmermann & Tomlinson, 1967). There are corresponding differences in the leaf-contact distance, with major bundles many internodes long, and minor bundles only a few. In addition to the 100 vascular leaf traces, there are about 1000 cortical bundles. These appear last and, by definition, diverge only from the stem cortex. They are discontinuous basipetally or anastomose among themselves.

The "rules" that govern vascular development in major bundles also apply to later-formed bundles, except that maturation of cell types occurs later. Differentiation of vascular tissues in progressively more peripheral (minor) bundles takes place during shorter periods of extension; consequently, minor leaf traces have very little protoxylem. Metaxylem matures somewhat later than in major bundles but according to the same principles. Although it would be possible to quantify these statements with the techniques available, no fundamentally novel information would be obtained.

DISCUSSION

The information presented above, when considered together with our previous studies on the course and structure of vascular bundles in mature stems and the process of initiation of vascular bundles themselves, allows us to present a highly integrated view of vascular development in the palm crown. Vascular bundles establish continuity between stem and leaf as procambial strands and increase in number at the level of leaf insertion. When a bundle makes contact with a leaf in this way, protophloem and metaxylem elements are already differentiated in the lower part of its course; the differentiation and maturation of these tissues is continuous acropetally, but metaxylem matures in such a way that it diverges into bridges or branch traces and does not continue along the leaf trace proper into the leaf base.

Protoxylem first appears in the distal part of the trace when the associated leaf is in position P2. It is discontinuous both distally into the leaf and proximally into the axial portion of the leaf trace. Protoxylem continuous from stem to leaf first occurs when the leaf is at about position P7.

Metaxylem does not begin to mature until the subtending internode of a given leaf has ceased to elongate. However, younger leaves have an indirect vascular continuity with the axial metaxylem because mature protoxylem and metaxylem are contiguous in completely mature internodes, with the mature protoxylem distally continuous through actively extending tissues and into the leaf itself (FIGURE 8). Xylem contact of about four or five leaves with expanded blades is made through tissue extension in this way. This means that the xylem-to-xylem contact between stem and leaf is still developing after the leaf blade has expanded. Sperry (pers. comm.) has preliminary information showing that this change affects the transpirational capacity of the leaf in its early life as an expanded organ.

HYDRAULIC CONSIDERATIONS

Transport capacity in the xylem to the developing leaf is indicated approximately by FIGURE 7 as the total number of protoxylem elements in the leaf base at successive plastochrones, which is at first dependent on—and then subsequently independent of—the total number of vascular bundles that differentiate in the leaf base. The measure is incomplete and would be better indicated by the sum of the fourth power of the diameter of all elements (Zimmermann & Sperry, 1983). The basipetal connection of this protoxylem is dependent on the overlap between protoxylem and metaxylem at lower levels.

The vertical distance over which metaxylem and protoxylem are directly contiguous within any one vascular bundle is limited. It may be termed the *vascular insertion* of the leaf trace onto the axial system (Sperry, pers. comm.), in contrast to the *morphological insertion* of the leaf base at the node itself. Only in the region of overlap can water move directly from metaxylem into the protoxylem of leaf traces; this, therefore, is the significant level of leaf insertion as far as water transport is concerned. However, vascular continuity between axial and leaf-trace xylem is established very late in crown development, in internodes in which extension has just been completed. It is dependent

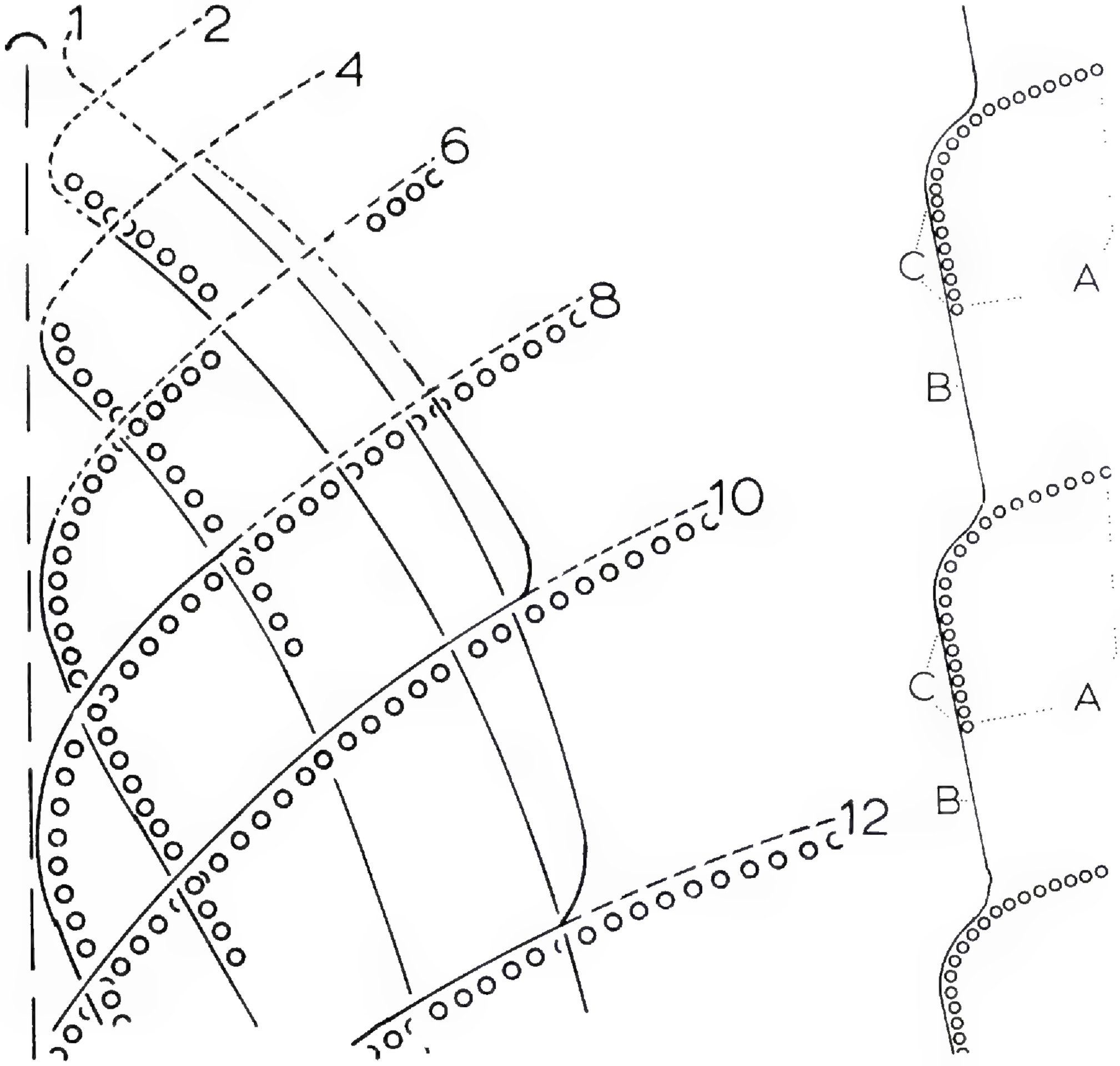

FIGURE 8. *Rhapis excelsa*, fundamental aspects of xylem development and topography. Left: developmental relationships between procambium (dotted lines), protoxylem (hollow circles), and differentiating metaxylem (solid line) in crown. (Numbers = leaf positions, topographic relationships schematic—see FIGURES 5, 6.) Right: relationship between protoxylem (hollow circles) and metaxylem (solid line) in mature stem; 2 complete leaf contacts of major stem vascular bundle. (A = "foliar" component of xylem system—protoxylem continuous into leaf base but discontinuous below in stem; B = "cauline" component of xylem system, permitting axial continuity in stem but not directly continuous into leaf; C = region of overlap between A and B where mature protoxylem and metaxylem in direct contact (region of "vascular" insertion within stem, in contrast to "morphological" insertion of leaf at node).)

on elements differentiating late as protoxylem, next to metaxylem elements in which maturation has just been completed. Distally, water moves into leaves only through protoxylem, as in the traces to P8, 10, 12, and 13 in FIGURE 5.

Major bundles that have extensive protoxylem connection with the leaf base continue to develop new tracheary elements between first-formed protoxylem and still-immature metaxylem within extending regions. Over the region of

vascular insertion (i.e., where protoxylem and metaxylem are laterally contiguous), differentiation of protoxylem continues from initials adjacent to immature metaxylem elements. The water-transport pathway is only completed when metaxylem finally matures.

Dissection of a number of crowns showed that there are four or five incompletely mature leaves (in which the leaf blade is expanded but the base is still immature) older than the spear leaf. The internodes below the node of insertion of each of these leaves is also still extending. Consequently, the first fully mature leaf associated with the first fully mature internode is about the fifth below the spear leaf and about P13 in this crown as a whole. All internodes below this level are completely extended and support fully mature leaves. The total number of leaves in the crown varies according to the position of the crown: fully exposed crowns include fewer visible and enclosed leaves (about nine of each), while those in the shade support more visible and enclosed leaves (about twelve of each). This range of quantitative variation has to be considered when absolute statements are made about the level of vascular differentiation below the shoot apex. Time of maturation of tissues may vary by as much as three plastochrones in different crowns. Nevertheless, similar conditions determine the development of the hydraulic connection established in each leaf as it develops.

COMPARISON WITH OTHER MONOCOTYLEDONS

The most directly comparable study is that by Esau (1943) of the ontogeny of the vascular bundle in *Zea mays*. Although there are some common features, there are also appreciable divergences in the process of vascular bundle development between this grass and the palm studied here because of differences between them in size and general organization. A particular difference is in the axial meristem: it is interrupted in the stem of corn, and uninterrupted in the palm (see Fisher & French, 1976). The corn stem thus has a nodal plexus that is absent from the palm. Consequently, Esau was not concerned with the topographic differences between different bundles within the internode since these are largely controlled by the activity of the intercalary stem meristem, and she gave a detailed account of bundle development in leaves, which is not considered here. Despite this, similar features of development in the two plants include the method of early development of the procambium and the early appearance of protophloem and protoxylem at opposite poles of the strand (FIGURE 2). Increase in diameter of the bundle in both plants occurs by tangential longitudinal division that produces radial seriation of cells in transverse sections of the bundle (e.g., FIGURE 2, D). Esau considered it inappropriate to view this as a "cambium" (an opinion with which we concur) since this implies homologies with vascular organization that are not likely to exist in dicotyledons. That this is not a cambium is clear from the observation that division occurs during elongation of the vascular bundle. FIGURE 2, D, for example, in which radial seriation is particularly obvious, represents a level only 1 mm below the shoot apex, whereas extension occurs over an additional distance of several centimeters (cf. FIGURES 1 and 5).

Esau indicated that at any one level, protophloem always appears first, pro-

toxylem second. This sequence is common in stem bundles in *Rhapis,* but it is not always followed due to the greater topographic complexity. Protoxylem may precede protophloem (FIGURE 2, C) in the differentiation of leaf traces, and metaxylem initiation in axial bundles may even precede initiation of protophloem. Metaxylem initials, of course, are not totally mature until much later, after axial elongation is complete.

Despite these differences, some general features of vascular differentiation in *Rhapis*—including the continuous acropetal differentiation of phloem and metaxylem—correspond to those found in other angiosperms. In contrast, protoxylem is discontinuously differentiated within each bundle, originating in the distal part of each leaf trace and, in a relative sense, rapidly extending both acropetally and basipetally. The protoxylem of the proximal leaf trace must advance acropetally in the stem to make contact with the distal protoxylem of the bundle in the leaf base. Although it is reasonable to assume topographic advance of further protoxylem differentiation in a basipetal direction, we have not estimated this quantitatively against fixed reference points. There is never continuity between protoxylem of one trace and that of another. This discontinuity is a topographic consequence of the acropetal advance of the cessation of internodal elongation and a direct expression of stem growth via an uninterrupted meristem. Continuity of the xylem transport pathway is effected by the juxtaposition of metaxylem and the last-formed protoxylem. This is the basis for the "hydraulic constriction" at each leaf insertion, recognized by Zimmermann and Sperry (1983) and illustrated in Zimmermann *et al.* (1982), upon which the whole hydraulic architecture of the palm is based. This simple developmental arrangement is reinforced by the failure of metaxylem to differentiate in the outgoing leaf trace beyond the level of departure of the last bridge or axial bundle.

PHLOEM DIFFERENTIATION

Unlike Esau, in her study of *Zea* (1943), we have been unable to make a very clear distinction between protophloem and metaphloem. In *Zea* the latter is structurally distinct because only metaphloem includes companion cells and its elements are arranged in regular radial series. Such a distinction is not evident in *Rhapis.* However, if we accept that metaphloem, by definition, only matures after the bundle is completely elongated, it is clear from FIGURE 5 that all the phloem differentiated in the crown is protophloem. Obliteration of first-formed protophloem is extensive, but some passive extension can presumably be accommodated. Since metaphloem and protophloem are not topographically distinct (unlike protoxylem and metaxylem), continuity of development is evident.

LEAF TRACE AND AXIAL BUNDLE

We have used the terms "axial bundle" and "leaf trace" without precise definition in this series of papers. "Leaf trace" refers to the outwardly curved portion of a bundle shortly before its entry into the leaf base, and "axial bundle" to the portion of a bundle remote from its entry into a leaf. With progressive

increase in our understanding of the topography, initiation, and differentiation of vascular bundles, the terms can now be refined somewhat. In a topographic sense, the axial bundle can be said to become a leaf trace either at the point of its maximum level of penetration into the stem center or at the level of departure of the continuing axial bundle. The latter is unsatisfactory because this varies considerably in different monocotyledons: the leaf trace would be very short in some because the axial bundle departs close to the stem periphery, and in others because a distinct axial bundle is not always present (Zimmermann & Tomlinson, 1974, *fig. 9*).

In developmental terms the level at which the "basipetally" determined influence of the leaf conjoins the "acropetally" determined influence of the meristematic cap could represent the junction of the two portions of a subsequently continuous vascular bundle. This definition is difficult to apply, although it may have the most precise morphogenetic meaning. It corresponds closely to the first topographic definition.

In histological and functional terms, the "leaf trace" can be defined precisely as that portion of the stem bundle over which protoxylem differentiates (FIGURE 8). This definition is readily accommodated by structural analysis and has direct functional significance because it is the basis for the hydraulic constriction mentioned by Zimmermann and Sperry (1983). The definition differs from both preceding ones because the "axial bundle" (represented by the metaxylem) and the "leaf trace" (represented by the protoxylem) necessarily overlap considerably. The "axial bundle" is continuous along the stem and makes no direct contact with the leaf. We thus have a precise developmental and functional application of the abstract and much-debated notion of the "cauline bundle" (Esau, 1965). The "cauline" portion corresponds to the axial vasculature in which metaxylem is differentiated, since this is the pathway for axial movement of water up the stem (FIGURE 8, B). The "foliar" portion (FIGURE 8, A) is the leaf trace in the above protoxylic context and, at least in a palm, relates solely to the irrigation of the major appendages (the leaves) via the region of direct contact (FIGURE 8, C).

Protoxylem discontinuity appears to be a universal developmental feature of stem vascular tissues (Esau, 1965) but has not previously been explained in a functional sense. Hydraulic architecture gives a possible clue. At times of stress, xylem dysfunction is restricted to disposable plant parts while axial continuity is preserved (cf. Zimmermann, 1983).

From this analysis and its functional application, we can extract information that can be applied to vascular plants generally. For example, analyses of *Populus* show similarity in the time of appearance of vascular tissues and the development of hydraulic constrictions (Larson, 1976, 1982; Larson & Isebrands, 1978). However, these features are much condensed in the apical region: events that occur over distances of a few hundred microns in *Populus* (Larson, 1975) extend over centimeters and throughout many plastochrones in palms. This is the basis for our suggestion that palms are particularly suitable organisms for studying vascular development.

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THE TREATMENT OF AUBLET'S GENERIC NAMES BY HIS CONTEMPORARIES AND BY PRESENT-DAY TAXONOMISTS

JAMES L. ZARUCCHI

IN 1775 Aublet published his *Histoire des Plantes de la Guiane Françoise,* an illustrated account of his botanical studies in the French colony between 1762 and 1764. In this work Aublet described many new species and introduced 208 new genera of plants to science. In a recent work, Howard (1983) dealt with the identities of the plants illustrated in the 392 plates in the work, reviewed the various taxonomic problems or uncertainties concerning the identities of some of Aublet's species, and presented a selected list of critical references that consider Aublet or the plants that he collected and described.

The purpose of the present paper is to review how several botanists who were contemporary with Aublet treated his 208 genera. Scopoli, in his *Introductio ad Historiam Naturalem* (1777), and Schreber, in the two-volume eighth edition of Linnaeus's *Genera Plantarum* (1789, 1791), proposed many new generic names as replacements for names of Aublet that they considered "vulgar or barbarous" (Stafleu, 1971). Although neither Scopoli nor Schreber treated all of Aublet's genera, A. L. de Jussieu, another contemporary botanist, reviewed all 208 generic names in his *Genera Plantarum* (1789) and placed nearly all of them within his system of natural families. Many additional replacement names for Aublet's taxa were provided by Necker in his three-volume *Elementa Botanica* (1790). Necker's names are not treated in this paper since his "species naturalis" are considered to be monomial names for species and therefore not validly published (Stafleu & Cowan, 1981). The Sydney Code (Voss *et al.*, 1983) supports this view of the nomenclatural status of Necker's names under Article 20.4(b).

In addition to publishing the 208 generic names in his *Histoire des Plantes de la Guiane Françoise,* Aublet validated the pre-Linnaean name *Clompanus* of Rumphius, by describing a second species under that genus. The nomenclatural and taxonomic problems associated with *Clompanus* [Rumph.] Aublet are presently being studied by Geesink (pers. comm.).

TABLE 1 presents Aublet's 208 generic names in alphabetical order; lists their treatment according to Scopoli (1777), Schreber (1789, 1791), and Jussieu (1789); and gives their current disposition as presented by Howard (1983). Modifications or explanations are added where needed. Footnotes supply any additional nomenclatural or taxonomic information necessary.

TABLE 2 provides an index by entry number to all of the generic names

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TABLE 1. **The nomenclatural and taxonomic treatments of Aublet's generic names by Scopoli (1777), Schreber (1789, 1791), and Jussieu (1789), and their current taxonomic status.**[1]

Aublet (1775)	Scopoli (1777)[2]	Schreber (1789, 1791)[2]	Jussieu (1789)[3]	Current Status[4]
1. +Aberemoa (ANNO) (=*Duguetia A. St. Hil. [1824]) ("Aberemo" in T [531])	NC	NC	= Cananga Aublet	Guatteria Ruiz & Pavon (1794)[5]
2. Ablania (ELAE)	Ablania Aublet	÷ Trichocarpus Schreber (1789)	Ablania Aublet	Sloanea L. (1753)
3. Abuta (MENI)	NC	NC	Abuta Aublet	Abuta Aublet[6]
4. Acioa (CHRY) ("Acioua" in T [678])	Acioa Aublet ("Acioia" in I)	÷ Acia Schreber (1791) (with Couepia Aublet; as "Conepia" in T, corr. in Addenda)	Acioa Aublet	Acioa Aublet
5. +Acouroa (LEGU) (=*Dalbergia L. f. [1781])	"Acovrea" Aublet ("Acourea in I)	NC	Acouroa Aublet (with Vatairea Aublet in S)	? *Dalbergia L. f. (1781)[7]
6. Aiouea (LAUR)	÷ Ehrhardia Scop. ("Aiovea" in S)	÷ +Douglassia Schreber (1791)[8]	"Ajovea" Aublet	Aiouea Aublet
7. Amaioua (RUBI) ("Amaïoua" on P)	NC	NC	"Amaïoua" Aublet[§]	Amaioua Aublet
8. Amanoa (EUPH)	Amanoa Aublet	NC	Amanoa Aublet	Amanoa Aublet
9. Ambelania (APOC)	= Benteca Adanson (1763) ("Ambelamia" in I)	÷ +Willughbeja Schreber (1789, 1791)[9] (with Pacouria Aublet)	Ambelania Aublet	Ambelania Aublet
10. Aniba (LAUR)	Aniba Aublet	÷ Cedrota Schreber (1789)	Aniba Aublet	Aniba Aublet
11. +Apalatoa (LEGU) ("Opalatoa" on P) (=*Crudia Schreber [1789])	÷ Waldschmidtia Scop.	÷ Cyclas Schreber (1789) (with Iouchiroa Aublet)	Apalatoa Aublet (Touchiroa in S)	*Crudia Schreber (1789)

12. Apeiba (TILI)	Apeiba Aublet	÷ #Aubletia Schreber (1789)[10] (with Sloanea "Loefl.")	Apeiba "Marcg. Aubl." (with Sloanea L. [1753] in S)	Apeiba Aublet
13. Arouna (LEGU)	"Arovna" Aublet	NC	Arouna Aublet	Dialium L. (1767)
14. Aruba (SIMA)	"Arvba" Aublet	NC	Aruba Aublet	Simaba Aublet
15. *Bacopa (SCRO)[11]	= Bellonia L. (1753)	Bacopa Aublet	Bacopa Aublet	*Bacopa Aublet
16. Bagassa (MORA)	NC	NC	Bagassa Aublet	Bagassa Aublet
17. Baillieria (COMP) ("Bailleria" in T [793])	"Bailliaria" Aublet ("Baillaria" in I)	= #Trixis Sw. (1788)[12] ("Bailliera" in S)	"Ballieria" Aublet	Clibadium L. (1771)
18. Banara (FLAC)	Banara Aublet	Banara Aublet	Banara Aublet	Banara Aublet
19. Bassovia (SOLA)	Bassovia Aublet	Bassovia Aublet	Bassovia Aublet	Solanum L. (1753)
20. Bertiera (RUBI)	Bertiera Aublet	Bertiera Aublet	Bertiera Aublet	Bertiera Aublet
21. Bocoa (LEGU)	NC	NC	Bocoa Aublet[§]	Bocoa Aublet
22. Cabomba (CABO)	Cabomba Aublet	÷ Nectris Schreber (1789)	Cabomba Aublet	Cabomba Aublet
23. Cacoucia (COMB)	÷ Hambergera Scop. ("Cacoutia" in S)	NC	Cacoucia Aublet	*Combretum Loefl. (1758)
24. Calinea (DILL)	Calinea Aublet	= Doliocarpus Rolander (1756)	Calinea Aublet	Doliocarpus Rolander (1756)
25. +Cananga (ANNO) (=*Guatteria Ruiz & Pavon [1794])	Cananga Aublet	NC	Cananga Aublet (with Uvaria longifolia Sonn. & Aberemoa Aublet in S)	*Guatteria Ruiz & Pavon (1794)
26. Caraipa (BONN) ("Caraipe" in T [531])	NC	NC	Caraipa Aublet (Caraïpa in I)	Caraipa Aublet[13]
27. Carapa (MELI)	NC	NC	Carapa Aublet[§]	Carapa Aublet

TABLE 1 (*continued*).

Aublet (1775)	Scopoli (1777)[2]	Schreber (1789, 1791)[2]	Jussieu (1789)[3]	Current Status[4]
28. +Carapichea (RUBI) (=*Cephaëlis Sw. [1788])	÷ Chesnea Scop.	÷ Callicocca Schreber (1789) (with Tapogomea Aublet & Evea Aublet [*Cephaëlis Sw. (1788) is added as a S in the "Addenda et Emendanda" (1791)])	= Tapogomea Aublet	*Psychotria L. (1759)
29. Cassipourea (RHIZ)	÷ Tita Scop.	= Legnotis Sw. (1788)[14]	Cassipourea Aublet	Cassipourea Aublet
30. Catinga (MYRT) ("Catringa" in I)	NC	NC	Catinga Aublet	? Calycorectes O. Berg (1856)[15]
31. Ciponima (SYMP) ("Siponima" on P)	"Siponima" Aublet	= Symplocos Jacq. (1760) ("Siponima" in S)	Ciponima Aublet	Symplocos Jacq. (1760)
32. Cipura (IRID)	"Cipvra" Aublet	÷ Marica Schreber (1789)	Cipura Aublet	Cipura Aublet
33. Conami (EUPH)	NC	NC	Conami Aublet§	Phyllanthus L. (1753)
34. Conceveiba (EUPH) ("Couceveiba" in T [891], I, & on P)	NC	NC	Conceveiba Aublet§	Conceveiba Aublet
35. Conobea (SCRO)	Conobea Aublet	÷ Conopea Schreber (1791) ("Conolea" in I)	Conobea Aublet	Conobea Aublet
36. (+)Conohoria (VIOL)[16]	Conohoria Aublet ("Conohria" in I)	NC	÷ Conoria A. L. Juss.	(*)Rinorea Aublet[16]
37. +Coublandia (LEGU) (=*Muellera L. f. [1781])	= ?Caesalpinia L. (1753)	NC	Coublandia Aublet	*Muellera L. f. (1781)
38. Couepia (CHRY)	NC	÷ Acia Schreber (1791) (with Acioa Aublet; as "Conepia" in S, corr. in Addenda)	Couepia Aublet	Couepia Aublet
39. Couma (APOC)	NC	NC	Couma Aublet§	Couma Aublet

40. +Coumarouna (LEGU) (=*Dipteryx Schreber [1791])	≠ Heinzia Scop.	≠ *Dipteryx Schreber (1791) (with Taralea Aublet)	Coumarouna Aublet	*Dipteryx Schreber (1791)
41.(+)Coupoui (RUBI)[17]	NC	NC	Coupoui Aublet§	*Duroia L. f. (1781)[17]
42. Couratari (LECY)	NC	NC	= Zanonia L. (1753)	Couratari Aublet
43. Courimari (?ELAE)	NC	NC	Courimari Aublet§	? Sloanea L. (1753)[18]
44. Couroupita (LECY)	≠ Pontopidana Scop. ("Coroupita" in S)	NC	Couroupita Aublet	Couroupita Aublet
45. Coussapoa (CECR)	NC	NC	Coussapoa Aublet	Coussapoa Aublet
46. Coussarea (RUBI)	≠ Pecheya Scop.	NC	Coussarea Aublet	Coussarea Aublet
47. Coutarea (RUBI)	"Covtarea" Aublet	NC	Coutarea Aublet (with Portlandia "Jacq. L." [P. Br.] [1756] in S)	Coutarea Aublet
48. Coutoubea (GENT)	≠ Limborchia Scop.	≠ Picrium Schreber (1791)	Coutoubea Aublet	Coutoubea Aublet
49. Crenea (LYTH)	"Crena" Aublet	"Crenaea" Aublet ("Cranea" in I)	Crenea Aublet	Crenea Aublet
50. +Deguelia (LEGU) (=*Derris Lour. [1790])	"Degvelia" Aublet	NC	Deguelia Aublet	*Derris Lour. (1790)
51. Enourea (SAPI)	"Enovrea" Aublet	NC	Enourea Aublet	Paullinia L. (1753)
52. Eperua (LEGU)	"Eperva" Aublet	≠ Dimorpha Schreber (1791) (with Parivoa Aublet)	Eperua Aublet	Eperua Aublet
53. +Evea (RUBI) (=*Cephaëlis Sw. [1788])	Evea Aublet	≠ Callicocca Schreber (1789) (with Tapogomea Aublet & Carapichea Aublet)	Evea Aublet	Faramea Aublet
54. Faramea (RUBI)	= Knoxia L. (1753)	NC	Faramea Aublet	Faramea Aublet
55. +Ferolia (MORA) (=*Brosimum Sw. [1788])	NC	NC	= Parinarium A. L. Juss. (see under no. 117)	*Brosimum Sw. (1788)

TABLE 1 (*continued*).

Aublet (1775)	Scopoli (1777)[2]	Schreber (1789, 1791)[2]	Jussieu (1789)[3]	Current Status[4]
56. #Fothergilla (MELA)[19]	≠ +Leonicenia Scop.[20]	= Melastoma L. (1753) (with various genera in S)	= Melastoma "Burm. L."	*Miconia Ruiz & Pavon (1794)
57. Galipea (RUTA)	NC	NC	"Galipaea" Aublet	Galipea Aublet
58. Goupia (GOUP)	"Govpia" Aublet ("Guopia" in I)	≠ Glossopetalum Schreber (1789)	Goupia Aublet	Goupia Aublet
59. Guapira (NYCT) ("Quapira" on P)	"Gvapira" Aublet	~~NC~~	= Avicennia L. (1753)	Pisonia L. (1753)
60. Hevea (EUPH)	NC	≠ Siphonia D. Rich. ex Schreber (1791)	= Jatropha L. (1753)	Hevea Aublet
61. Heymassoli (OLAC)	≠ +Rottboelia Scop.[21]	NC	= Ximenia "Pl. L." (1753)	Ximenia L. (1753)
62. +Houmiri (HUMI) (=*Humiria Aublet corr. J. St. Hil. [1805]) ("Homiri" in T [531])	≠ Wernisekia Scop.	≠ Myrodendrum Schreber (1789)	≠ Houmiria A. L. Juss.	*Humiria Aublet corr. J. St. Hil. (1805)
63. +Icacorea (MYRS) (=*Ardisia Sw. [1788])	NC	NC	Icacorea Aublet[§]	*Ardisia Sw. (1788)[22]
64. Icica (BURS)	Icica Aublet	NC	Icica Aublet	Protium Burm. f. (1768)
65. Iroucana (FLAC)	≠ Moelleria Scop.	≠ #Athenaea Schreber (1789)[23]	= Anavinga "Rheed. Lam."	Casearia Jacq. (1760)
66. Ivira (STER) ("Iuira on P)	Ivira Aublet	= Sterculia L. (1753)	= Sterculia L. (1753)	Sterculia L. (1753)
67. Licania (CHRY)	Licania Aublet	≠ Hedycrea Schreber (1789)	Licania Aublet	Licania Aublet
68. Licaria (LAUR)	NC	NC	Licaria Aublet[§]	Licaria Aublet
69. Mabea (EUPH)	Mabea Aublet	Mabea Aublet	Mabea Aublet	Mabea Aublet

70. Macahanea (?CELA)	NC	NC	≠ Macanea A. L. Juss.	? Salacia L. (1771)
71. Macoubea (APOC)	NC	NC	Macoubea Aublet	Macoubea Aublet
72. Macoucoua (AQUI)[24] ("Maracoua" in T [53])	≠ +Labatia Scop.[25] ("Macoucaua" Aublet in T & "Macoucava" in I)	NC	= Ilex L. (1753)	Ilex L. (1753)
73. Mahurea (BONN)	"Mahvrea" Aublet	≠ +Bonnetia Schreber (1789)[26] ("Mahuria" Aublet in T & I)	Mahurea Aublet	Mahurea Aublet
74. Maieta (MELA) ("Mayeta" in T [368] & on P)	Maieta Aublet	= Melastoma L. (with various genera in S) ("Mayeta" Aublet in T & I)	"Mayeta" Aublet	Maieta Aublet
75. Malanea (RUBI)	= Chomelia L. (1758)	≠ +Cunninghamia Schreber (1791)[27] ("Malanca" in I; with "Antirrhea Commers.?")	Malanea Aublet	Malanea Aublet
76. Manabea (VERB)	= Pavetta L. (1753) [RUBI]	= Aegiphila Jacq. (1767)	Manabea Aublet	Aegiphila Jacq. (1767)
77. Managa (?CELA)	NC	NC	Managa Aublet[§]	? Salacia L. (1771)
78. Mapania (CYPE)	Mapania Aublet	NC	Mapania Aublet	Mapania Aublet
79. Mapouria (RUBI)	"Mapovria" Aublet	NC	= Simira Aublet	*Psychotria L. (1759)
80. Maprounea (EUPH) ("Mapronnea" on P)	NC	= Aegopricum L. (1775)	Maprounea Aublet	Maprounea Aublet
81. Maquira (MORA)	NC	NC	Maquira Aublet[§]	Maquira Aublet
82. Maripa (CONV)	NC	NC	Maripa Aublet	Maripa Aublet
83. Matayba (SAPI) ("Mataïba" on P)	≠ Ernstingia Scop.	≠ Ephielis Schreber (1789) ("Mataïba" in T & I)	Matayba Aublet ("Mataïba" in I)	Matayba Aublet
84. Matelea (ASCL)	Matelea Aublet	NC	Matelea Aublet	Matelea Aublet
85. Matourea (SCRO)	"Matovrea" Aublet (gen. 706) ≠ Dickia Scop. (gen. 877)	= Vandellia P. Br. [ex L.] (1767)	Matourea Aublet	*Stemodia L. (1759)

TABLE 1 (*continued*).

Aublet (1775)	Scopoli (1777)[2]	Schreber (1789, 1791)[2]	Jussieu (1789)[3]	Current Status[4]
86. Mayaca (MAYA) ("Maiaca" on P)	Mayaca Aublet	÷ Syena Schreber (1789)	Mayaca Aublet	Mayaca Aublet
87. +Mayepea (OLEA) (=*Linociera Sw. ex Schreber [1791]) ("Mayepa" in I)	÷ Freyeria Scop. ("Mayepa" Aublet in S)	÷ +Ceranthus Schreber (1789)	Mayepea Aublet	Chionanthus L. (1753)[28]
88. Mayna (FLAC)	NC	NC	Mayna Aublet	Mayna Aublet
89. Meborea (EUPH)	Meborea Aublet	÷ Rhopium Schreber (1791)	Meborea Aublet	? Phyllanthus L. (1753)
90. Minquartia (OLAC)	NC	NC	Minquartia Aublet[§]	Minquartia Aublet
91. Montira (LOGA)	Montira Aublet ("Montiva" in I)	NC	Montira Aublet	Spigelia L. (1753)
92. Moquilea (CHRY)	÷ "Dahyronia" Scop. ("Moguilea" in S)	NC	Moquilea Aublet	Licania Aublet
93. Moronobea (GUTT)	÷ Blakstonia Scop.[29]	= Symphonia L. f. (1781)	Moronobea Aublet	Moronobea Aublet
94. Mourera (PODO)	"Movrera" Aublet	÷ Lacis Schreber (1789)	Mourera Aublet	Mourera Aublet
95. Mouriri (MELA)	÷ Bockia Scop. ("Movriri" in S)	= Myrtus L. (1753) (with various genera in S) (gen. 844 in 1789) = Petaloma Sw. (1788) (gen. 1750 in 1791)	"Mouriria" Aublet	Mouriri Aublet
96. Mouroucoa (CONV) ("Mouroucoua" in I)	÷ Maireria Scop.	NC	Mouroucoa Aublet	Maripa Aublet
97. Moutabea (POLY) ("Moutoubea" in I)	NC	÷ Cryptostomum Schreber (1789)	Moutabea Aublet	Moutabea Aublet

98. Moutouchi (LEGU)	≠ Griselinia Scop. ("Mourouchi" in I)	NC	= +Pterocarpus "Loefl. L."[30] ("Moutouchiam" in S; "Moutouchia" in I)	*Pterocarpus Jacq. (1763)
99. Nacibea (RUBI)	Nacibea Aublet	= *Manettia Mutis [ex L.] (also cited +Lygistum P. Br. [1756] in S)	Nacibea Aublet (*Mannetia "Mut. L." [1771] in S)	*Manettia Mutis ex L. (1771)
100. Napimoga (FLAC)	≠ Tattia Scop.	NC	Napimoga Aublet	Homalium Jacq. (1760)
101. Nonatelia (RUBI)	Nonatelia Aublet	≠ Oribasia Schreber (1789)	Nonatelia Aublet	*Psychotria L. (1759)
102. Norantea (MARC)	Norantea Aublet	≠ Ascium Schreber (1789)	Norantea Aublet	Norantea Aublet
103. Ocotea (LAUR)	Ocotea Aublet	≠ Porostema Schreber (1791) (with *Nectandra Rolander [ex Rottb.][1778])	Ocotea Aublet	Ocotea Aublet
104. ≠Orelia (APOC) (illeg. name based on Allamanda L. [1771])	= Gentiana L. (1753) (with Chlora [Adanson] [1763] and Swertia L.)	= Allamanda L. (1771) (with "Galarips Auth. D. Allamand." [ex L.])	= Allamanda L. (1771)	Allamanda L. (1771)
105. *Ouratea (OCHN)[31]	"Ovratea" Aublet	NC	Ouratea Aublet	*Ouratea Aublet
106. +Ourouparia (RUBI) (=*Uncaria Schreber [1789])	= Genipa L. (1754)	≠ *Uncaria Schreber (1789)	= Nauclea L. (1762)	*Uncaria Schreber (1789)
107. +Outea (LEGU) (=*Macrolobium Schreber [1789])	"Ovtea" Aublet	≠ *Macrolobium Schreber (1789) (with Vouapa Aublet)	Outea Aublet	*Macrolobium Schreber (1789)
108. Pachira (BOMB)	Pachira Aublet	= Carolinea L. [f.] (1781)[32]	Pachira Aublet[33]	Pachira Aublet
109. +Pacouria (APOC) (=*Landolphia P. Beauv. [1805])	≠ +Alstonia Scop.[34]	≠ +Willughbeja Schreber[35] (1789, corr. 1791) (with Ambelania Aublet)	Pacouria Aublet	+Pacouria Aublet
110. Pacourina (COMP)	≠ Meisteria Scop.	NC	Pacourina Aublet	Pacourina Aublet
111. Pagamea (RUBI) ("Pagama" in T [113]; corr. in Addenda)	NC	NC	Pagamea Aublet	Pagamea Aublet

TABLE 1 (*continued*).

Aublet (1775)	Scopoli (1777)[2]	Schreber (1789, 1791)[2]	Jussieu (1789)[3]	Current Status[4]
112. Palicourea (RUBI)	= Simira Aublet ("Polycourea" in S, T, I)	÷ Stephanium Schreber (1789) ("Palicourex" in S, corr. in Addenda [1791])	= Simira Aublet (with Mapouria Aublet)	Palicourea Aublet
113. Paloue (LEGU) ("Palove" in I)	÷ Ginannia Scop.	= Ginannia Scop. (1777) ("Paloue" Aublet in T & I)	÷ Palovea A. L. Juss. (with "Paloue" Aublet in S)	Paloue Aublet
114. [+]Pamea (COMB)[36]	NC	NC	Pamea Aublet	Buchenavia Eichler (1866)[36]
115. Paralea (EBEN)	NC	NC	Paralea Aublet	Diospyros L. (1753)
116. Pariana (GRAM)	Pariana Aublet	Pariana Aublet	Pariana Aublet	Pariana Aublet
117. Parinari (CHRY)	÷ "Dygortia" Scop.	÷ Petrocarya Schreber (1789)	÷ Parinarium A. L. Juss. (with Ferolia Aublet)	Parinari Aublet
118. Parivoa (LEGU)	Parivoa Aublet	÷ Dimorpha Schreber (1791) (with Eperua Aublet)	Parivoa Aublet	Eperua Aublet
119. Passoura (VIOL)	NC	NC	= Riana Aublet	Rinorea Aublet
120. Patabea (RUBI)	- +"Sicelivm" P. Br. (1756)[37] (with Tontanea Aublet)	NC	Patabea Aublet	Ixora L. (1753)
121. Patima (RUBI)	NC	NC	Patima Aublet	Patima Aublet
122. Paypayrola (VIOL)	÷ Lignonia Scop.	NC	÷ Payrola A. L. Juss.	Paypayrola Aublet
123. Pekea (CARY)	Pekea Aublet	÷ Rhizobolus Gaertner ex Schreber (1789)	Pekea Aublet (with Saouari Aublet in S)	Caryocar L. (1771)
124. Perama (RUBI)	NC	÷ Mattuschkaea Schreber (1791)	Perama Aublet	Perama Aublet
125. Perebea (MORA)	Perebea Aublet ("Peribea" in I)	NC	Perebea Aublet	Perebea Aublet

126. Piparea (FLAC)	NC	NC	Piparea Aublet	Casearia Jacq. (1760)
127. +Piratinera (MORA) (=*Brosimum Sw. [1788])	NC	NC	Piratinera Aublet§	*Brosimum Sw. (1788)
128. ÷Pirigara (LECY)[38]	Pirigara Aublet	= *Gustavia L. (1775)	Pirigara Aublet (with Gustavia "LS." in S)	*Gustavia L. (1775)[38]
129. Piripea (SCRO)	Piripea Aublet	= Buchnera L. (1753)	Piripea Aublet	Buchnera L. (1753)
130. Piriqueta (TURN)	÷ "Bvrghartia" Scop. ("Pariqueta" in S)	= "Burcardia" Scop.	Piriqueta Aublet	Piriqueta Aublet
131. Pitumba (FLAC)	NC	÷ +Wolfia Schreber (1791)[39]	Pitumba Aublet§	Casearia Jacq. (1760)
132. Poraqueiba (ICAC)	÷ #Barreria Scop.[40] ("Paraqueiba" in S)	= #Barreria Scop. (1777)[40]	Poraqueiba Aublet ("Poraqueïba" in I)	Poraqueiba Aublet
133. Posoqueria (RUBI)	÷ Ramspekia Scop. ("Posogueria" in S)	÷ Cyrtanthus Schreber (1789)	Posoqueria Aublet	Posoqueria Aublet
134. +Possira (LEGU) (=*Swartzia Schreber [1791])	Possira Aublet	÷ Rittera Schreber (1789)	Possira Aublet	*Swartzia Schreber (1791)
135. Potalia (LOGA)	Potalia Aublet	÷ #Nicandra Schreber (1789)[41]	Potalia Aublet	Potalia Aublet
136. Pourouma (CECR)	NC	NC	Pourouma Aublet	Pourouma Aublet
137. Pouteria (SAPO)	Pouteria Aublet	÷ +Chaetocarpus Schreber[42] (gen. 179 in 1789) = *Labatia Sw. (1788)[43] (gen. 1724 in 1791)	Pouteria Aublet	Pouteria Aublet
138. Qualea (VOCH)	"Qvalea" Aublet	Qualea Aublet	Qualea Aublet	Qualea Aublet
139. Quapoya (GUTT)	÷ +Smithia Scop.[44] ("Gvapoya" in S)	÷ Xanthe Schreber (1791)	Quapoya Aublet	Quapoya Aublet
140. Quararibea (BOMB)	÷ #Gerberia Scop.[45] ("Quaraïbea" in S; "Quaraiba" in I)	= Myrodia Sw. (1788)[46]	Quararibea Aublet	Quararibea Aublet

TABLE 1 (*continued*).

Aublet (1775)	Scopoli (1777)[2]	Schreber (1789, 1791)[2]	Jussieu (1789)[3]	Current Status[4]
141. Quebitea (PIPE)	NC	NC	= Dracontium L. (1753) [ARAC]	Piper L. (1753)
142. Quiina (QUII)	NC	NC	Quiina Aublet[§]	Quiina Aublet
143. Racaria (SAPI)	NC	NC	Racaria Aublet[§]	Talisia Aublet
144. Racoubea (FLAC)	÷ "Lagvnezia" Scop.	= Homalium Jacq. (1760)	= Homalium Jacq. (1760)	Homalium Jacq. (1760)
145. Rapanea (MYRS)	= Plotia Adanson (1763)	NC	Rapanea Aublet	Myrsine L. (1753)
146. Rapatea (RAPA)	Rapatea Aublet	÷ Mnasium Schreber (1789)	Rapatea Aublet	Rapatea Aublet
147. Raputia (RUTA)	"Rapvtia" Aublet	÷ Sciuris Schreber (1789)	Raputia Aublet	Raputia Aublet
148. [+]Remirea (CYPE)[47]	"Remeira" Aublet	÷ Miegia Schreber (1791)	Remirea Aublet	*Mariscus Vahl (1805/6)[47]
149. Riana (VIOL)	= Rinorea Aublet	NC	Riana Aublet (with Passoura Aublet in S)	Rinorea Aublet
150. (*)Rinorea (VIOL)[48]	Rinorea Aublet (with Riana Aublet in S)	NC	Rinorea Aublet	(*)Rinorea Aublet[48]
151. Ronabea (RUBI) ("Ronobea" in I & on P)	"Ronobea" Aublet	NC	Ronabea Aublet	*Psychotria L. (1759)
152. Ropourea (EBEN)[49]	÷ +Idesia Scop.[50]	÷ Camax Schreber (1789)	Ropourea Aublet	Diospyros L. (1753)
153. Rouhamon (LOGA)	÷ Chemnicia Scop. ("Rohamon" in S)	÷ Lasiostoma Schreber (1789)	= Strychnos L. (1753) (with Ignatia "LS." [L. f.] [1781] & "Caniram Rheed." in S)	Strychnos L. (1753)
154. Roupala (PROT)	÷ Leinkeria Scop.	"Rhopala" Aublet	Roupala Aublet	Roupala Aublet
155. *Rourea (CONN)[51]	"Rovrea" Aublet	÷ Robergia Schreber (1789)	Rourea Aublet	*Rourea Aublet

156. Sabicea (RUBI)	= Hamelia Jacq. (1760)	÷ Schwenkfelda Schreber (1789) (gen. 306) ÷ Schwenkfeldia Schreber (1791) (corr. in Addenda)	Sabicea Aublet	Sabicea Aublet
157. Sagonea (HYDR)	Sagonea Aublet	÷ Reichelia Schreber (1789) ("Sagona" in S) = *Hydrolea L. (1762) (author as "Sw.")	Sagonea Aublet	*Hydrolea L. (1762)
158. Saouari (CARY)	NC	NC	= Pekea Aublet	Caryocar L. (1771)
159. Senapea (?PASS)	NC	NC	Senapea Aublet[§]	? Senapea Aublet
160. Simaba (SIMA)	Simaba Aublet	÷ #Zwingera Schreber (1791)[52]	Simaba Aublet	Simaba Aublet
161. *Simarouba (SIMA)[53]	NC	NC	= Quassia L. (1762)	Simarouba Aublet
162. Simira (RUBI)	Simira Aublet	NC	Simira Aublet (with Mapouria Aublet & Palicourea Aublet in S)	Simira Aublet
163. Singana (?LEGU)	Singana Aublet	÷ Sterbeckia Schreber (1789)	Singana Aublet	? Singana Aublet
164. Sipanea (RUBI)	Sipanea Aublet	= Virecta L. (1775)[54]	= Mussaenda L. (1753)[55]	Sipanea Aublet
165. Siparuna (MONI)	NC	NC	Siparuna Aublet	Siparuna Aublet
166. Soramia (DILL) ("Saramia" in T [531])	Soramia Aublet	= Doliocarpus Rolander (1756) (gen. 874 in 1789) ÷ #Mappia Schreber[56] (gen. 1755 in 1791)	Soramia Aublet	Doliocarpus Rolander (1756)
167. Souroubea (MARC)	÷ +Loghania Scop.[57]	= Ruyschia Jacq. (1760)	Souroubea Aublet	Souroubea Aublet
168. Tachia (GENT)	Tachia Aublet	÷ Myrmecia Schreber (1789)	Tachia Aublet	Tachia Aublet
169. Tachibota (CHRY)	NC	÷ Salmasia Schreber (1789)	Tachibota Aublet	Hirtella L. (1753)
170. Tachigali (LEGU)	÷ "Cvba" Scop.	= "Cubaea" Scop. (1777)	"Tachigalia" Aublet	Tachigali Aublet[58]

TABLE 1 (*continued*).

Aublet (1775)	Scopoli (1777)[2]	Schreber (1789, 1791)[2]	Jussieu (1789)[3]	Current Status[4]
171. +Taligalea (VERB) (=*Amasonia L. f. [1781])	Taligalea Aublet	= *Amasonia L. [f.] (1781)	Taligalea Aublet	*Amasonia L. f. (1781)
172. Talisia (SAPI)	Talisia Aublet	NC	Talisia Aublet	Talisia Aublet
173. Tamonea (VERB)[59]	Tamonea Aublet	÷ Ghinia Schreber (1789)	Tamonea Aublet (with "Verbena L." [1753] in S)	Tamonea Aublet[59]
174. Tampoa (CELA)	NC	NC	Tampoa Aublet[§]	? Tampoa Aublet
175. Tanibouca (COMB)	NC	NC	Tanibouca Aublet	Terminalia L. (1767)
176. +Taonabo (THEA) (=*Ternstroemia Mutis ex L. f. [1781])	÷ "Dvpinia" Scop.	= *Ternstroemia Mutis ex L. [f.] (1781) (with additional genera in S)	÷ Tonabea A. L. Juss.	*Ternstroemia Mutis ex L. f. (1781)
177. Tapirira (ANAC)	"Taparira" Aublet	÷ Joncquetia Schreber (1789)	"Tapiria" Aublet	Tapirira Aublet
178. +Tapogomea (RUBI) (=*Cephaëlis Sw. [1788])	Tapogomea Aublet	÷ Callicocca Schreber (1789) (with Carapichea Aublet & Evea Aublet)	Tapogomea Aublet (with Carapichea Aublet in S)	*Psychotria L. (1759)
179. Tapura (DICH)	"Tapvra" Aublet	÷ Rohria Schreber (1789)	Tapura Aublet	Tapura Aublet
180. +Taralea (LEGU) (=*Dipteryx Schreber [1791])	Taralea Aublet	÷ *Dipteryx Schreber (1791) (with Coumarouna Aublet)	Taralea Aublet	*Dipteryx Schreber (1791)
181. +Tariri (SIMA) (=*Picramnia Sw. [1788])	NC	NC	= Comocladia "Brown. L. Jacq." [P. Br.] (1756) (with Pseudo-Brasilium "HRP." [Adanson (1763)] in S)	*Picramnia Sw. (1788)
182. Thoa (GNET)	Thoa Aublet	Thoa Aublet	Thoa Aublet	Gnetum L. (1767)

183. Tibouchina (MELA)	÷ Savastania Scop. ("Tibochina" in I)	= Melastoma L. (1753) (with various genera in S)	Tibouchina Aublet	Tibouchina Aublet
184. Ticorea (RUTA)	Ticorea Aublet	÷ Ozophyllum Schreber (1791)	Ticorea Aublet	Ticorea Aublet
185. Tigarea (DILL)	"Tigvrea" Aublet	÷ Rhinium Schreber (1791)[60]	Tigarea Aublet	Tetracera L. (1753)
186. Tococa (MELA)	Tococa Aublet	= Melastoma L. (1753) (with various genera in S)	Tococa Aublet	Tococa Aublet
187. Tocoyena (RUBI)	?= Genipa L. (1754)[61]	NC	Tocoyena Aublet	Tocoyena Aublet
188. Tonina (ERIO)	Tonina Aublet	÷ Hyphydra Schreber (1791)	Tonina Aublet	Tonina Aublet
189. Tontanea (RUBI)	= +"Sicelivm" P. Br. (1756) (with Patabea Aublet)	÷ #Bellardia Schreber (1791)[62]	Tontanea Aublet	*Coccocypselum P. Br. (1756) corr. Schreber (1791)
190. Tontelea (CELA)	"Tontalea" Aublet	÷ Tonsella Schreber (1789)	Tontelea Aublet	Tontelea Aublet
191. Topobea (MELA)	Topobea Aublet	NC	Topobea Aublet	Topobea Aublet
192. +Touchiroa (LEGU) (=*Crudia Schreber [1789])	NC	÷ Cyclas Schreber (1789) (with Apalatoa Aublet)	= Apalatoa Aublet	*Crudia Schreber (1789)
193. Toulicia (SAPI) ("Toulipita" in T [324])	"Tovlicia" Aublet	÷ Ponaea Schreber (1789)	Toulicia Aublet	Toulicia Aublet
194. +Tounatea (LEGU) (=*Swartzia Schreber [1791])	NC	÷ *Swartzia Schreber (1791)	Tounatea Aublet	*Swartzia Schreber (1791)
195. Touroulia (QUII)	÷ +Robinsonia Scop.[63]	= +Robinsonia Scop. (1777)	Touroulia Aublet	Touroulia Aublet
196. Tovomita (GUTT)	NC	NC	Tovomita Aublet	Tovomita Aublet
197. Trigonia (TRIG)	Trigonia Aublet	Trigonia Aublet	Trigonia Aublet	Trigonia Aublet
198. Vantanea (HUMI)	NC	÷ Lemniscia Schreber (1789)	Vantanea Aublet	Vantanea Aublet

TABLE 1 (*continued*).

Aublet (1775)	Scopoli (1777)[2]	Schreber (1789, 1791)[2]	Jussieu (1789)[3]	Current Status[4]
199. Vatairea (LEGU) ("Voitairea" in T [730])	NC	NC	= Acouroa Aublet	Vatairea Aublet
200. Virola (MYRI)	Virola Aublet	= "Myristica Thunb." [*Myristica Gronov. (1755)]	Virola Aublet	Virola Aublet
201. +Vochy (Voch) (=*Vochysia Aublet corr. Poiret [1808] [nom. & orth. cons.])	÷ Salmonia Scop. ("Vochi" in T; "Vochy" in I)	÷ Cucullaria Schreber (1789)	÷ Vochisia A. L. Juss.	*Vochysia Aublet corr. Poiret (1808)
202. Votomita (MELA)	Votomita Aublet	÷ Glossoma Schreber (1791)	Votomita Aublet	Votomita Aublet
203. +Vouacapoua (LEGU) (=*Andira A. L. Juss. [1789])	NC	NC	= Andira "Pif. Lamark." [Lam. ex A. L. Juss.] ("Angelin Pl." in S)	+Vouacapoua Aublet
204. +Vouapa (LEGU) (=*Macrolobium Schreber [1789])	÷ "Krvegeria" Scop.	÷ *Macrolobium Schreber (1789) (with Outea Aublet)	Vouapa Aublet	*Macrolobium Schreber (1789)
205. Vouarana (SAPI)	NC	NC	= Ornitrophe Comm. [ex A. L. Juss.] ("Voua-rana" Aublet in S)	Vouarana Aublet
206. Voyara (CAPP)	NC	NC	Voyara Aublet[§]	Capparis L. (1753)
207. Voyria (GENT)	Voyria Aublet	÷ Lita Schreber (1791)	"Vohiria" Aublet	Voyria Aublet
208. Xiphidium (HAEM)	"Xiphidivm" Aublet	Xiphidium "Loefling. Aubl."	Xiphidium "Loefl. Aubl."	Xiphidium Aublet

[1]This Table lists Aublet's 208 generic names in alphabetical order, followed by a four-letter abbreviation for the family (see Table 3). Conserved genera are preceded by an asterisk (*), rejected names by a plus sign (+), superfluous names by "÷," and later homonyms by "#." In the case of a rejected name, its conserved counterpart is listed below that entry in the first column. Orthographic variants appear in quotes, followed by their location in the relevant publication: text (T), index (I), or plate (P). Names appearing in synonymy are cited as "in S."

[2]Scopoli and Schreber did not consider all of Aublet's genera in their treatments; the genera that were not cited (NC) are so noted.

[3]The names with a section symbol (§) indicate the genera listed by Jussieu (p. 446) under "OBS. Praeter genera ordinis indeterminati."

[4]According to the determinations provided by Howard (1983), except where noted. A question mark indicates doubt as to the identity or placement of a particular taxon.

[5]Although Howard (1983) gives the identification as Guatteria, he mentions the possibility that Aberemoa may actually represent a species of Duguetia, against which Aberemoa is rejected.

[6]See notes on the lectotypification of Abuta by Barneby & Krukoff (1971) and by Howard (1983).

[7]Howard (1983) indicates that there is no modern placement of Acouroa Aublet; the genus is rejected in favor of Dalbergia L. f.

[8]Not +Douglassia Miller (1754) -- Verbenaceae.

[9]Schreber attributed the authorship of +Willughbeja (not *Willughbeia Roxb. [1820] -- Apocynaceae) to Scopoli in Volume 1 (1789), but later listed himself as the sole author in the Addenda found in Volume 2 (1791).

[10]Not Aubletia Gaertner (1788) -- Sonneratiaceae.

[11]Bacopa is conserved against +Moniera P. Br. (1756) and +Brami Adanson (1763) -- Scrophulariaceae.

[12]Not Trixis P. Br. (1756) -- Compositae; not #Trixis Adanson (1763) -- Haloragaceae.

[13]Of the four species of Caraipa described by Aublet, only the lectotype species, C. parvifolia Aublet, is a member of the Bonnetiaceae. The remaining species represent members of Licania and Couepia (Chrysobalanaceae); see Howard (1983) and Kubitzki (1978) for further details.

[14]Legnotis was proposed by Swartz (1788) as a replacement name for Cassipourea Aublet.

[15]For references relating to the identity of Catinga (with lectotype species C. moschata Aublet), see Howard (1983). If Catinga Aublet and Calycorectes O. Berg prove to be congeneric, then a choice must be made either to conserve the latter name or to make the appropriate combinations under Catinga.

[16]Hekking (1982) proposes that Rinorea Aublet be conserved over Conohoria Aublet.

[17]A proposal to conserve Duroia L. f. over Coupoui Aublet will be submitted to Taxon (Zarucchi, in prep.).

[18]The identity of Courimari Aublet as a species of Sloanea L. is highly questionable; see Howard (1983) for further comments.

[19]Not Fothergilla L. (1774) -- Hamamelidaceae. Howard (1983) provides an account of the change from Tamonea (Melastomataceae) to Fothergilla while Aublet's work was being printed. Close inspection of various copies of Aublet (1775) has shown that several pages in the work were replaced after the initial page impressions.

[20]Leonicenia Scop. is rejected in favor of *Miconia Ruiz & Pavon (1794) -- Melastomataceae.

[21]Not *Rottboellia L. f. (1780) -- Gramineae.

[22]In a recent article, Lundell (1981) accepts Icacorea Aublet as distinct from Ardisia Sw. and published approximately one hundred combinations in Icacorea.

[23]Not +Athenaea Adanson (1763) -- Compositae; not *Athenaea Sendtner (1846) -- Solanaceae.

[24]In Index Nominum Genericorum, Farr and colleagues (1979) list the family as Celastraceae.

[25]Not *Labatia Sw. (1788) -- Sapotaceae.

[26]Not *Bonnetia Martius (1826) -- Bonnetiaceae.

[27]Not *Cunninghamia R. Br. (1826) -- Taxodiaceae.

[28]For details regarding the taxonomic standing of Mayepea Aublet, Linociera Sw. ex Schreber, and Chionanthus L., see Stearn (1976).

[29]Not Blackstonia Hudson (1762) -- Gentianaceae.

[30]Not *Pterocarpus Jacq. (1763) -- Leguminosae.

[31]Ouratea Aublet is conserved, but no genus is listed as rejected in favor of Ouratea; see Voss et al. (1983).

[32]Carolinea L. f. is an illegitimate name; it was superfluous when published.

[33]Carolinea "L.S." is listed as a replacement generic name.

[34]Not *Alstonia R. Br. (1810) -- Apocynaceae.

[35]See notes regarding this replacement name under Ambelania (entry no. 9).

[36]If Pamea Aublet and Buchenavia Eichler are indeed congeneric, then either Buchenavia should be proposed for conservation or the appropriate combinations under Pamea should be made.

[37]Sicelium P. Br. is rejected in favor of *Coccocypselum P. Br. (1756) corr. Schreber (1791).

[38]Pirigara was illegitimate when published since Japarandiba (a Marcgrave name validly published by Adanson in 1763) was listed in synonymy under Pirigara tetrapetala Aublet; Gustavia L. is conserved against Japarandiba Adanson.

[39]Not *Wolffia Horkel ex Schleiden (1844) -- Lemnaceae.

[40]Not Barreria L. (1753) -- Rutaceae.

[41]Not *Nicandra Adanson (1763) -- Solanaceae.

[42]Not *Chaetocarpus Thwaites (1854) -- Euphorbiaceae.

[43]Not +Labatia Scop. (1777), a replacement name for Macoucoua Aublet (Aquifoliaceae) (see entry no. 72).

[44]Not *Smithia Aiton (1784) -- Leguminosae.

[45]Not *Gerbera L. (1758) -- Compositae.

[46]Swartz (1788) introduced Myrodia as a replacement name for Quararibea Aublet.

[47]Howard (1983) reports that the monotypic Remirea Aublet (1775) and Mariscus Vahl (1805/6) are congeneric. A proposal will be made to add Remirea to the list of genera rejected in favor of Mariscus (Zarucchi, in prep.); Mariscus Vahl is already conserved against +Mariscus Scop. (1754) -- Cyperaceae.

[48]Hekking (1982) proposes that Rinorea Aublet be conserved over Conohoria Aublet (see entry no. 36).

[49]In Index Nominum Genericorum, Farr and colleagues (1979) list Ropourea Aublet and the replacement names of Scopoli and Schreber as members of the Verbenaceae rather than the Ebenaceae.

[50]Not *Idesia Maxim. (1866) -- Flacourtiaceae.

[51]Rourea is conserved against +Kalawael Adanson (1763).

[52]Not Zwingeria Heister ex Fabr. (1759) -- Labiatae; not Zwingera Hofer (1762) -- Nolanaceae.

[53]Not +Simaruba Boehmer (1760) -- Burseraceae.

[54]Schreber (1789), as well as Farr and colleagues (1979), incorrectly attributed the publication of Virecta to Linnaeus filius in the Supplementum Plantarum (1781 [1782]); Virecta was first published by Linnaeus in Plantae Surinamenses (1775).

[55]With Landia Comm. [ex A. L. Juss.] in synonymy.

[56]Not +Mappia Heister ex Fabr. (1759) -- Labiatae; not *Mappia Jacq. (1797) -- Icacinaceae.

[57]Not *Logania R. Br. (1810) -- Loganiaceae.

[58]This name of Aublet appears in much of the botanical literature as "Tachigalia."

[59]Tamonea is accepted as a validly published name of verbenaceous plants. See comments under Fothergilla Aublet (entry no. 56) and in Howard (1983) and Stafleu & Cowan (1976).

[60]Rhinium Schreber appears as genus number 1545 in the text; in "Addenda et Emendanda" Schreber listed "1545. RHINIUM. Deleatur."

[61]Based on genus number citation in the index; not listed in the text.

[62]Not Bellardia All. (1785) -- Scrophulariaceae.

[63]Not *Robinsonia DC. (1833) -- Compositae.

TABLE 2. **Index to generic names listed in Table 1.**[1]

Aberemoa Aublet - 1f[2], 25
Abuta Aublet - 3f
Acia Schreber - 4, 38
Acioa Aublet - 38
Acouroa Aublet - 5f, 199
Aegiphila Jacq. - 76
Aegopricum L. - 80
Allamanda L. - 104
Alstonia R. Br. - 109f
Alstonia Scop. - 109
Amasonia L. f. - 171
Ambelania Aublet - 109, 109f
Anavinga Adanson - 65
Andira A. L. Juss. - 203
Antirhea Comm. ex A. L. Juss. - 75
Apalatoa Aublet - 192
Ardisia Sw. - 63, 63f
Ascium Schreber - 102
Athenaea Adanson - 65f
Athenaea Schreber - 65
Athenaea Sendtner - 65f
Aubletia Gaertner - 12f
Aubletia Schreber - 12
Avicennia L. - 59
Bacopa Aublet - 15f
Barreria L. - 132f
Barreria Scop. - 132
Bellardia All. - 189f
Bellardia Schreber - 189
Bellonia L. - 15
Benteca Adanson - 9
Blackstonia Hudson - 93f
Blakstonia Scop. - 93
Bockia Scop. - 95
Bonnetia Martius - 73f
Bonnetia Schreber - 73
Brami Adanson - 15f
Brosimum Sw. - 55, 127
Buchenavia Eichler - 114, 114f
Buchnera L. - 129
Burghartia Scop. - 130
Caesalpinia L. - 37
Callicocca Schreber - 28, 53, 178
Calycorectes O. Berg - 30, 30f
Camax Schreber - 152
Cananga Aublet - 1
Capparis L. - 206
Caraipa Aublet - 26f
Carapichea Aublet - 53, 178
Carolinea L. f. - 108, 108f
Caryocar L. - 123, 158
Casearia Jacq. - 65, 126, 131
Cassipourea Aublet - 29f
Catinga Aublet - 30f
Cedrota Schreber - 10
Cephaëlis Sw. - 28, 53, 178
Ceranthus Schreber - 87
Chaetocarpus Schreber - 137
Chaetocarpus Thwaites - 137f
Chemnicia Scop. - 153
Chesnea Scop. - 28
Chionanthus L. - 87, 87f
Chlora Adanson - 104
Chomelia L. - 75
Clibadium L. - 17
Coccocypselum P. Br. corr. Schreber - 120f, 189
Combretum Loefl. - 23
Comocladia P. Br. - 181
Conohoria Aublet - 36f, 150f
Conopea Schreber - 35
Conoria A. L. Juss. - 36
Couepia Aublet - 4, 26f
Coumarouna Aublet - 180
Coupoui Aublet - 41f
Courimari Aublet - 43f
Crudia Schreber - 11, 192
Cryptostomum Schreber - 97
Cuba Scop. - 170
Cucullaria Schreber - 201
Cunninghamia R. Br. - 75f
Cunninghamia Schreber - 75
Cyclas Schreber - 11, 192
Cyrtanthus Schreber - 133
Dahuronia Scop. - 92
Dalbergia L. f. - 5, 5f
Derris Lour. - 50
Dialium L. - 13
Dickia Scop. - 85
Dimorpha Schreber - 52, 118
Diospyros L. - 115, 152
Dipteryx Schreber - 40, 180
Doliocarpus Rolander - 24, 166
Douglassia Miller - 6f
Douglassia Schreber - 6
Dracontium L. - 141
Dugortia Scop. - 117
Duguetia A. St. Hil. - 1, 1f
Dupinia Scop. - 176
Duroia L. f. - 41, 41f
Ehrhardia Scop. - 6
Eperua Aublet - 118
Ephielis Schreber - 83
Ernstingia Scop. - 83
Evea Aublet - 28, 178
Faramea Aublet - 53
Ferolia Aublet - 117
Fothergilla Aublet - 173f
Fothergilla L. - 56f
Freyeria Scop. - 87
Galarips Allam. ex L. - 104
Genipa L. - 106, 187
Gentiana L. - 104

TABLE 2 (*continued*).

Gerbera L. - 140f
Gerberia Scop. - 140
Ghinia Schreber - 173
Ginannia Scop. - 113
Glossoma Schreber - 202
Glossopetalum Schreber - 58
Gnetum L. - 182
Griselinia Scop. - 98
Guatteria Ruiz & Pavon - 1, 1f, 25
Gustavia L. - 128, 128f
Hambergera Scop. - 23
Hamelia Jacq. - 156
Hedycrea Schreber - 67
Heinzia Scop. - 40
Hirtella L. - 169
Homalium Jacq. - 100, 144
Houmiria A. L. Juss. - 62
Humiria Aublet corr. J. St. Hil. - 62
Hydrolea L. - 157
Hyphydra Schreber - 188
Icacorea Aublet - 63f
Idesia Maxim. - 152f
Idesia Scop. - 152
Ignatia L. f. - 153
Ilex L. - 72
Ixora L. - 120
Japarandiba Adanson - 128f
Jatropha L. - 60
Joncquetia Schreber - 177
Kalawael Adanson - 155f
Knoxia L. - 54
Kruegeria Scop. - 204
Labatia Scop. - 72, 137f
Labatia Sw. - 72f, 137
Lacis Schreber - 94
Lagunezia Scop. - 144
Landia Comm. ex A. L. Juss. - 164f
Landolphia P. Beauv. - 109
Lasiostoma Schreber - 153
Legnotis Sw. - 29, 29f
Leinkeria Scop. - 154
Lemniscia Schreber - 198
Leonicenia Scop. - 56, 56f
Licania Aublet - 26f, 92
Lignonia Scop. - 122
Limborchia Scop. - 48
Linociera Sw. ex Schreber - 87, 87f
Lita Schreber - 207
Logania R. Br. - 167f
Loghania Scop. - 167
Lygistum P. Br. - 99
Macanea A. L. Juss. - 70
Macoucoua Aublet - 137f
Macrolobium Schreber - 107, 204
Maireria Scop. - 96
Manettia Mutis ex L. - 99
Mapouria Aublet - 112, 162
Mappia Heister ex Fabr. - 166f
Mappia Jacq. - 166f
Mappia Schreber - 166
Marica Schreber - 32
Maripa Aublet - 96
Mariscus Scop. - 148f
Mariscus Vahl - 148, 148f
Mattuschkaea Schreber - 124
Mayepea Aublet - 87f
Meisteria Scop. - 110
Melastoma L. - 56, 74, 183, 186
Miconia Ruiz & Pavon - 56, 56f
Miegia Schreber - 148
Mnasium Schreber - 146
Moelleria Scop. - 65
Moniera P. Br. - 15f
Muellera L. f. - 37
Mussaenda L. - 164
Myristica Gronov. - 200
Myrmecia Schreber - 168
Myrodendrum Schreber - 62
Myrodia Sw. - 140, 140f
Myrsine L. - 145
Myrtus L. - 95
Nauclea L. - 106
Nectandra Rolander ex Rottb. - 103
Nectris Schreber - 22
Nicandra Adanson - 135f
Nicandra Schreber - 135
Oribasia Schreber - 101
Ornitrophe Comm. ex A. L. Juss. - 205
Ouratea Aublet - 105f
Outea Aublet - 204
Ozophyllum Schreber - 184
Pacouria Aublet - 9
Palicourea Aublet - 162
Palovea A. L. Juss. - 113
Pamea Aublet - 114f
Parinarium A. L. Juss. - 55, 117
Parivoa Aublet - 52
Passoura Aublet - 149
Patabea Aublet - 189
Paullinia L. - 51
Pavetta L. - 76
Payrola A. L. Juss. - 122
Pecheya Scop. - 46
Pekea Aublet - 158
Petaloma Sw. - 95
Petrocarya Schreber - 117
Phyllanthus L. - 33, 89
Picramnia Sw. - 181
Picrium Schreber - 48
Piper L. - 141
Pirigara Aublet - 128f

Pisonia L. - 59
Plotia Adanson - 145
Ponaea Schreber - 193
Pontopidana Scop. - 44
Porostema Schreber - 103
Portlandia P. Br. - 47
Protium Burm. f. - 64
Pseudo-Brasilium Adanson - 181
Psychotria L. - 28, 79, 101, 151, 178
Pterocarpus Jacq. - 98, 98f
Pterocarpus L. - 98
Quararibea Aublet - 140f
Quassia L. - 161
Ramspekia Scop. - 133
Reichelia Schreber - 157
Remirea Aublet - 148f
Rhinium Schreber - 185, 185f
Rhizobolus Gaertner ex Schreber - 123
Rhopium Schreber - 89
Riana Aublet - 119, 150
Rinorea Aublet - 36, 36f, 119, 149, 150f
Rittera Schreber - 134
Robergia Schreber - 155
Robinsonia DC. - 195f
Robinsonia Scop. - 195
Rohria Schreber - 179
Ropourea Aublet - 152f
Rottboelia Scop. - 61
Rottboellia L. f. - 61f
Rourea Aublet - 155f
Ruyschia Jacq. - 167
Salacia L. - 70, 77
Salmasia Schreber - 169
Salmonia Scop. - 201
Saouari Aublet - 123
Savastania Scop. - 183
Schwenkfelda Schreber - 156
Schwenkfeldia Schreber - 156
Sciuris Schreber - 147
Sicelium P. Br. - 120, 120f, 189
Simaba Aublet - 14
Simaruba Boehmer - 161f
Simira Aublet - 79, 112
Siphonia D. Rich. ex Schreber - 60
Sloanea L. - 2, 12, 43, 43f
Smithia Aiton - 139f
Smithia Scop. - 139
Solanum L. - 19
Spigelia L. - 91
Stemodia L. - 85
Stephanium Schreber - 112
Sterbeckia Schreber - 163
Sterculia L. - 66
Strychnos L. - 153
Swartzia Schreber - 134, 194
Swertia L. - 104
Syena Schreber - 86
Symphonia L. f. - 93
Symplocos Jacq. - 31
Talisia Aublet - 143
Tamonea Aublet - 56f, 173f
Tapogomea Aublet - 28, 53
Taralea Aublet - 40
Tattia Scop. - 100
Terminalia L. - 175
Ternstroemia Mutis ex L. f. - 176
Tetracera L. - 185
Tita Scop. - 29
Tonabea A. L. Juss. - 176
Tonsella Schreber - 190
Tontanea Aublet - 120
Touchiroa Aublet - 11
Trichocarpus Schreber - 2
Trixis Adanson - 17f
Trixis P. Br. - 17f
Trixis Sw. - 17
Uncaria Schreber - 106
Uvaria L. - 25
Vandellia P. Br. ex L. - 85
Vatairea Aublet - 5
Verbena L. - 173
Virecta L. - 164, 164f
Vochisia A. L. Juss. - 201
Vochysia Aublet corr. Poiret - 201
Vouapa Aublet - 107
Waldschmidtia Scop. - 11
Wernisekia Scop. - 62
Willughbeia Roxb. - 9f
Willughbeja Schreber - 9, 9f, 109
Wolffia Horkel ex Schleiden - 131f
Wolfia Schreber - 131
Xanthe Schreber - 139
Ximenia L. - 61
Zanonia L. - 42
Zwingera Hofer - 160f
Zwingera Schreber - 160
Zwingeria Heister ex Fabr. - 160f

[1]Except Aublet's names appearing as main entries and only under that entry number in Table 1.
[2]Numbers followed by an "f" indicate that the generic name is discussed in a footnote to that entry number in Table 1.

TABLE 3. **List of Aublet's generic names by family.**[1]

Anacardiaceae [ANAC] - 177
Annonaceae [ANNO] - +1?, +25
Apocynaceae [APOC] - 9, 39, 71, ÷104, +109
Aquifoliaceae [AQUI] - 72
Asclepiadaceae [ASCL] - 84*
Bombacaceae [BOMB] - 108, 140
Bonnetiaceae [BONN] - 26*, 73
Burseraceae [BURS] - 64*
Cabombaceae [CABO] - 22
Capparaceae [CAPP] - 206
Caryocaraceae [CARY] - 123*, 158*
Cecropiaceae [CECR] - 45*, 136
Celastraceae [CELA] - ?70, ?77, 174?, 190
Chrysobalanaceae [CHRY] - 4, 38, 67, 92, 117*, 169
Combretaceae [COMB] - 23, [+]114, 175
Compositae [COMP] - 17*, 110
Connaraceae [CONN] - *155
Convolvulaceae [CONV] - 82, 96
Cyperaceae [CYPE] - 78, [+]148
Dichapetalaceae [DICH] - 179
Dilleniaceae [DILL] - 24, 166, 185*
Ebenaceae [EBEN] - 115, 152
Elaeocarpaceae [ELAE] - 2, ?43
Eriocaulaceae [ERIO] - 188
Euphorbiaceae [EUPH] - 8, 33, 34, 60, 69*, 80, 89?
Flacourtiaceae [FLAC] - 18, 65, 88, 100, 126, 131, 144
Gentianaceae [GENT] - 48*, 168, 207*
Gnetaceae [GNET] - 182
Goupiaceae [GOUP] - 58*
Gramineae [GRAM] - 116
Guttiferae [GUTT] - 93, 139*, 196
Haemadoraceae [HAEM] - 208
Humiriaceae [HUMI] - "62", 198
Hydrophyllaceae [HYDR] - 157
Icacinaceae [ICAC] - 132
Iridaceae [IRID] - 32
Lauraceae [LAUR] - 6, 10, 68, 103
Lecythidaceae [LECY] - 42, 44, ÷128*
Leguminosae [LEGU] - +5?, +11, 13, 21, +37, +40, +50, 52, 98, +107, 113, 118*, +134, ?163, 170*, +180, +192, +194, 199, +203, +204*
Loganiaceae [LOGA] - 91, 135, 153
Lythraceae [LYTH] - 49
Marcgraviaceae [MARC] - 102, 167
Mayacaceae [MAYA] - 86
Melastomataceae [MELA] - #56, 74, 95, 183, 186, 191, 202
Meliaceae [MELI] - 27
Menispermaceae [MENI] - 3*
Monimiaceae [MONI] - 165
Moraceae [MORA] - 16, +55, 81, 125, +127
Myristicaceae [MYRI] - 200
Myrsinaceae [MYRS] - +63, 145
Myrtaceae [MYRT] - 30*?
Nyctaginaceae [NYCT] - 59
Ochnaceae [OCHN] - *105
Olacaceae [OLAC] - 61, 90
Oleaceae [OLEA] - +87
Passifloraceae [PASS] - ?159
Piperaceae [PIPE] - 141
Podostemonaceae [PODO] - 94
Polygalaceae [POLY] - 97
Proteaceae [PROT] - 154
Quiinaceae [QUII] - 142, 195
Rapateaceae [RAPA] - 146
Rhizophoraceae [RHIZ] - 29
Rubiaceae [RUBI] - 7, 20, +28, (+)41, 46, 47, +53, 54*, 75, 79, 99*, 101*, +106, 111, 112, 120, 121, 124, 133, 151*, 156*, 162, 164, +178*, 187, 189
Rutaceae [RUTA] - 57, 147, 184
Sapindaceae [SAPI] - 51, 83, 143, 172, 193, 205
Sapotaceae [SAPO] - 137
Scrophulariaceae [SCRO] - *15, 35, 85, 129
Simaroubaceae [SIMA] - 14, 160, *161, +181
Solanaceae [SOLA] - 19
Sterculiaceae [STER] - 66
Symplocaceae [SYMP] - 31
Theaceae [THEA] - +176*
Tiliaceae [TILI] - 12*
Trigoniaceae [TRIG] - 197*
Turneraceae [TURN] - 130
Verbenaceae [VERB] - 76*, +171, 173

TABLE 3 (*continued*).

Violaceae [VIOL] - (+)36, 119, 122, 149, (*)150
Vochysiaceae [VOCH] - 138*, "201"

Family uncertain - ?43, ?70, ?77, ?159, ?163

[1]A listing by family of Aublet's 208 generic names treated in Table 1. The numbers indicate their current taxonomic acceptance (underlined) or treatment as a synonym (without underlining). Numbers corresponding to polytypic genera are followed by an asterisk (*), those of questionable status are followed by a question mark (?), and those accepted with a modified orthography appear in quotes ("). The five genera that are questionably placed in a family are both underlined and preceded by a question mark (?). Symbols preceding a generic number indicate a conserved name (*), a rejected name (+), a later homonym (#), or a name that was superfluous when published (÷). Parentheses or brackets around a symbol indicate that a proposal to conserve/reject has been (*) or should be [*] made.

(excluding main-entry names of Aublet) given in TABLE 1 and its footnotes. Finally, a review of the currently accepted taxonomic status for Aublet's genera, grouped by families, is presented in TABLE 3.

The orthography of taxonomic names varied frequently within and among the individual works of Aublet's time. Spelling variants and their location are listed in TABLE 1. Scopoli (1777) used "V" for both modern-day "U" and "V," and these variants are presented in quotation marks in TABLE 1. Article 73.5 of the Sydney Code (Voss *et al.*, 1983) has recently established that the use of "V" in this situation should not be considered nomenclaturally distinctive.

In Aublet's *Histoire des Plantes de la Guiane Françoise,* descriptions of representative species of his new genera were accompanied by separate line drawings. Most of these new genera (177 of 208) were monotypic, although others contained up to 6 species. The 31 polytypic genera described by Aublet (with the number of included species) are: *Abuta* (2), *Apeiba* (4), *Baillieria* (2), *Caraipa* (4), *Catinga* (2), *Coussapoa* (2), *Coutoubea* (2), *Faramea* (2), *Goupia* (2), *Icica* (6), *Mabea* (2), *Manabea* (3), *Matelea* (2), *Nacibea* (2), *Nonatelia* (6), *Parinari* (2), *Parivoa* (2), *Pekea* (2), *Pirigara* (2), *Qualea* (2), *Quapoya* (2), *Ronabea* (2), *Sabicea* (2), *Saouari* (2), *Tachigali* (2), *Taonabo* (2), *Tapogomea* (5), *Tigarea* (2), *Trigonia* (2), *Vouapa* (2), and *Voyria* (2).

In his *Introductio ad Historiam Naturalem,* Scopoli (1777) considered only 149 of Aublet's generic names and proposed replacements for 44. He accepted 90 genera and placed 13 in synonymy under previously described genera; 2 genera were treated as synonyms of other names of Aublet. Several of these replacement names were retained by Schreber (1789, 1791) in his edition of the *Genera Plantarum.* Others, however, were disregarded in favor of Schreber's own new names. In several cases Schreber took up names proposed by Swartz in his *Prodromus* (1788) or by Linnaeus *filius* in his *Supplementum*

Plantarum (1781). In addition, Schreber totally ignored 88 of Aublet's generic names. Together, Scopoli and Schreber considered 110 of Aublet's genera and ignored 49.

The *Genera Plantarum* by A. L. de Jussieu (1789) accounted for all of Aublet's 208 Neotropical genera of plants. For 8 genera, Jussieu proposed replacement names that were quite similar to Aublet's names; an additional 8 names were simply orthographic variants. Jussieu accepted a total of 182 of Aublet's genera, including the 8 similar replacement names. Twenty-six genera were considered to be taxonomic synonyms, with 8 of these synonyms of other genera of Aublet. Jussieu placed all except 20 genera in his "natural system" of classification.

The genera described by Aublet (1775) fall into 79 modern plant families if one views the questionably placed *Senapea* as a genus of Passifloraceae and if one accepts the Cecropiaceae and Goupiaceae. The best-represented families are the Rubiaceae and Leguminosae, with 26 and 21 of Aublet's genera attributed to them, respectively. No fewer than 9 accepted higher-plant family names are based on Aublet's generic names: Cabombaceae, Goupiaceae, Humiriaceae, Mayacaceae, Quiinaceae, Rapateaceae, Simaroubaceae, Trigoniaceae, and Vochysiaceae.

Many of Aublet's generic names have been the subject of conservation/ rejection proposals. Six of Aublet's names have been conserved (see TABLE 1, items 15, 62, 105, 155, 161, and 201). Two of these, *Houmiri* (62) and *Vochy* (201), are conserved with altered orthographies—*Humiria* and *Vochysia.* Hekking (1982) proposes to conserve one of Aublet's violaceous generic names, *Rinorea* (150), over another, *Conohoria* (36). *Ouratea* (105) has been conserved, but no name is listed as being rejected in its favor (Voss *et al.*, 1983).

Twenty-six of Aublet's generic names have been rejected, most of them apparently in favor of a more widely used or preferred name. Two of the rejected genera, *Pacouria* (109) and *Vouacapoua* (203), are considered to be taxonomically distinct from their conserved counterparts; two additional genera, *Aberemoa* (1) and *Acouroa* (5), may also fall into this category. During the course of the present investigation, it has come to my attention that three more of Aublet's genera need to be considered for rejection based on the identifications cited by Howard (1983). *Coupoui* (41) will be proposed for rejection in favor of *Duroia* L. f., and *Remirea* (148) in favor of *Mariscus* Vahl (Zarucchi, in prep.). *Pamea* (114), a monotypic genus when described by Aublet, is listed by Howard as a species of *Buchenavia* Eichler (1866) (Combretaceae), based upon a personal communication from Dr. C. Stace; it appears that a conservation/rejection proposal is in order. Another problem surrounds the correct identification of *Catinga moschata* Aublet, the generic lectotype of *Catinga* (McVaugh, 1956), which has been questionably identified as *Calycorectes bergii* Sandw. If *Calycorectes* O. Berg (1856) and *Catinga* prove to be congeneric, a rejection proposal may be desirable.

Two of Aublet's generic names, *Orelia* (104) and *Pirigara* (128), were illegitimate when published because they included the types of previously described genera. The description of *Orelia* Aublet contained the earlier-published

Allamanda L. (1771), and the protologue of *Pirigara* included *Japarandiba,* a Marcgrave name validly published by Adanson in 1763. *Japarandiba* is rejected in favor of *Gustavia* L. (1775). *Fothergilla* (56) is the only name used by Aublet that is a later homonym (of the hamamelidaceous *Fothergilla* L. (1774)) and therefore not acceptable. Of the remaining 167 genera, 52 are considered to be taxonomic synonyms of previously published genera and 115 are accepted. Only 7 of these 115 genera are accepted with reservation as to placement to family (43, 70, 77, 159, 163) or as to recognition as generically distinct within a family (89, 174).

Although current taxonomic opinion varies on the acceptance or rejection of some of Aublet's generic names, a large number of them are valid and in use today. The many unusual-sounding names published more than two centuries ago continue to fascinate, if not tongue-tie, new generations of tropical American botanists.

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VEGETATIVE ANATOMY AND THE TAXONOMIC STATUS OF ILEX COLLINA AND NEMOPANTHUS (AQUIFOLIACEAE)

PIETER BAAS

IN 1974 Clark clarified part of the confusion in the literature with respect to three deciduous North American species of *Ilex* L.: *I. longipes* Chapman, *I. decidua* Walter, and *I. collina* Alexander. Because *I. collina* has apopetalous corollas, calyx lobes that are semipersistent on the fruits and inconspicuous in staminate flowers, and free stamens, he transferred it to *Nemopanthus* Raf., noting that *I. longipes* as understood by most authors should be treated as a synonym of *Nemopanthus collinus*. In my accounts of the vegetative anatomy of the Aquifoliaceae (Baas, 1973, 1975, 1978), I noted the close anatomical similarities of *Nemopanthus* with several species of *Ilex* from subg. PRINUS (L.) Maxim. and concluded (1975, p. 355) that merging *Nemopanthus* with *Ilex* "would not meet with any opposition from vegetative anatomists," the peculiar cuticular markings of *Nemopanthus* leaves being the only distinguishing anatomical character.

Dudley and Eisenbeiss (U. S. National Arboretum) drew my attention to *Ilex collina* and expressed their view that the transfer to *Nemopanthus* by Clark might after all have been unjustified. In view of the desirability of a proper understanding of the affinities and taxonomic status of this species as well as of *Nemopanthus mucronatus* (L.) Trel., and also because of the potential or actual importance of these species in horticulture, leaf and xylem anatomy of *Ilex collina* was studied in considerable detail, and additional specimens of *Nemopanthus mucronatus* were examined in order to check the constancy (and hence the diagnostic and taxonomic value) of its anatomical characters.

MATERIALS AND METHODS

The techniques employed have been described earlier (Baas, 1973, 1975). Sections and macerations were studied by light microscopy, and gold-coated surfaces of critical-point dried, previously FAA-fixed material were examined with a scanning electron microscope. All material used for this study was from the herbarium or the living collections of the U. S. National Arboretum, Washington, D. C. The comparative part of the work is largely based on material from the Rijksherbarium collections, detailed previously (Baas, *op. cit.*).

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RESULTS

ILEX COLLINA

LEAF ANATOMY

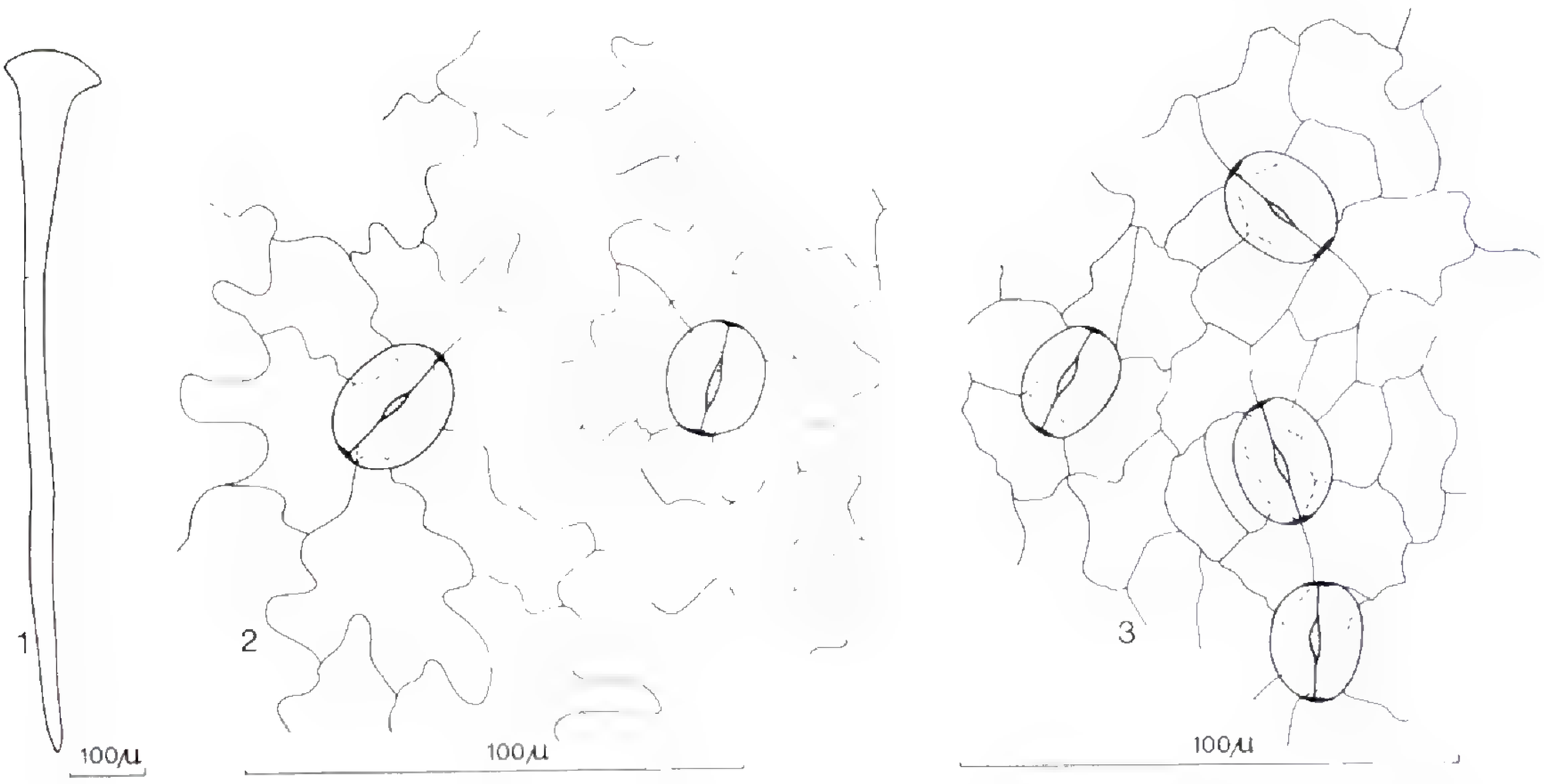
Material studied. U.S.A. Virginia: Mountain Lake, *Shanks s.n.* (NA). West Virginia: Cheat R., *Sharp 1070* (NA); Cheat Mt., *Hutton s.n.*, 13 Aug. 1940 (NA). Pennsylvania: cult. Arbor. Barnes Foundation, Merion, *Fogg s.n.* (NA). Washington, D. C.: cult. from seed collected in 1975 at type locality, *U. S. National Arboretum 38173* (NA); from seed collected in 1974, *Dudley & Eisenbeiss 400 1978* (NA); from seed collected in 1975, *U. S. National Arboretum s.n.* (alcohol-preserved material; L).

Surface view. Long, unicellular, partially septate hairs usually present, especially on veins and abaxial surface (FIGURE 1). Cuticle of adaxial and abaxial surfaces smooth to rather faintly striate (FIGURES 4, 5). Epidermal cells of adaxial surface with straight to (especially in leaves of juvenile specimens) undulating anticlinal walls, those of abaxial surface with strongly undulating (zigzag pattern) walls. Epidermal cell pattern modified over major veins and midrib only. Stomata confined to abaxial surface, irregularly anomocytic to cyclocytic with (3 or) 4 to 7 (to 10) neighboring/subsidiary cells (FIGURE 2), occasionally resembling anisocytic or laterocytic stomata (cf. Den Hartog–Van Ter Tholen & Baas, 1978), guard cell pairs (21–)26–32(–35) by (18–)20–26(–29) μm. Peristomal rims and cuticular T-pieces absent.

Transverse section. Lamina dorsiventral, 80–140 μm thick. Cuticle ca. 1 μm thick. Unspecialized epidermal cells usually flattened, the adaxial cells much larger than abaxial, often bulging, rarely with periclinal wall divisions and/or mucilaginous. Hypodermis absent. Mesophyll composed of 1 (rarely 2) layers of short to tall palisade cells and fairly loose spongy tissue. Midrib grooved adaxially, prominently raised abaxially, supplied with single shallowly arc-shaped collateral vascular bundle; vascular bundle with abaxial cap of thin-walled sclerenchyma fibers, very rarely (only in *Hutton s.n.*) with incurved margins. Ground tissue of midrib parenchymatous to collenchymatous. Veins mostly embedded, with parenchymatous bundle sheath poorly differentiated and extending to upper and lower epidermis only in major veins. Leaf margin with chlorenchymatous ground tissue. Petiole vascularization similar to that of midrib, proximal part with single bundle (type 1; cf. Baas, 1975), distal portion with additional small latero-dorsal wing bundles (types 3 and 4). Crystals present as druses especially in vicinity of vascular bundles.

WOOD ANATOMY

This description is based on a stem 6 mm in diameter from an alcohol-preserved specimen cultivated in the U. S. National Arboretum. Quantitative values should be considered with caution because the specimen was from an immature plant (3 years old). The presence of spiral thickenings was checked

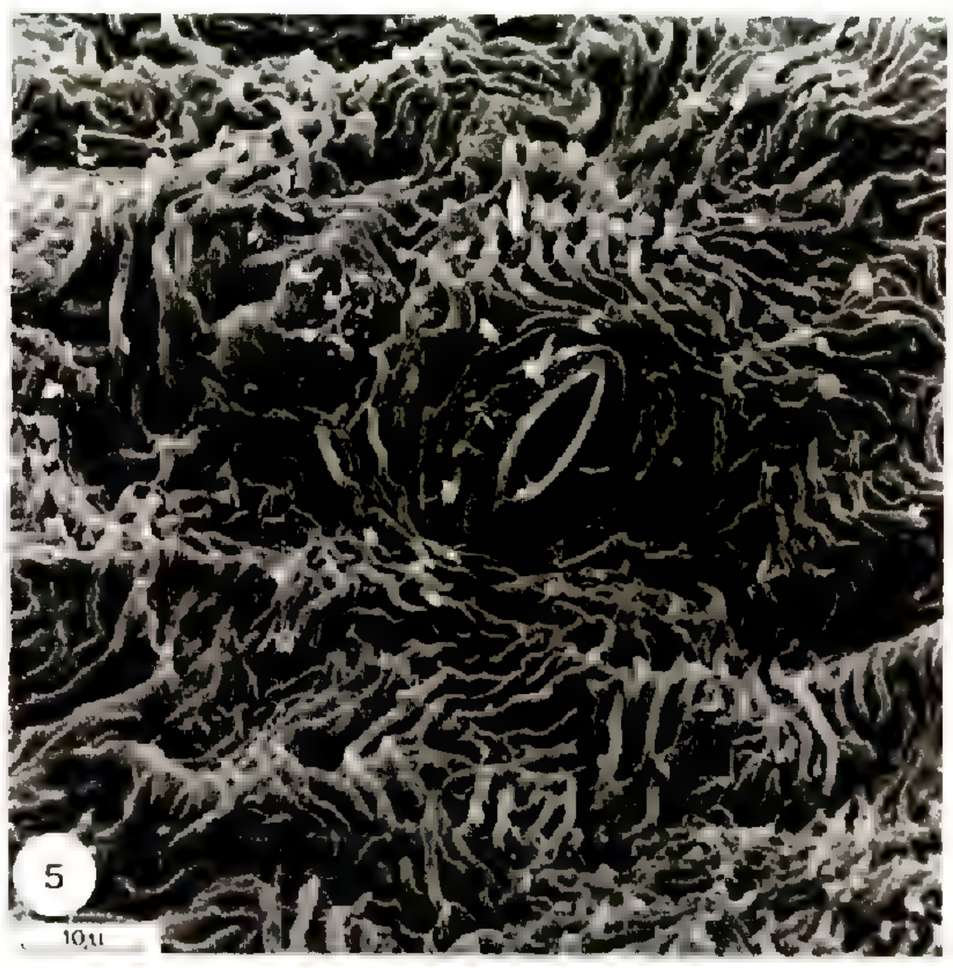


FIGURES 1–3. 1, 2, *Ilex collina:* 1, unicellular, septate hair; 2, anomocytic (left) and irregularly cyclocytic (right) stomatal complex. 3, *Nemopanthus mucronatus,* cyclocytic, anomocytic, and laterocytic stomata.

and confirmed in thin twigs of all herbarium specimens used in studying the leaf anatomy (see above).

Wood semi–ring porous. Growth rings distinct. Vessels ca. 160 per mm^2, solitary (ca. 30%) and in radial multiples of 1 to 6, angular to oval in transverse section, tangential diameter (17–)27(–40) μm, vessel member length (270–)540(–690) μm. Intervessel pits mainly opposite (some transitional or tending to alternate), oval or elongate, 5–8 μm in horizontal diameter, with slitlike apertures enclosed within pit borders. Vessel–ray and vessel–parenchyma pits similar but half bordered. Perforations scalariform in oblique end walls with (11–)14(–20) bars. Spiral thickenings well developed (FIGURE 6). Vessel contents and tyloses absent. Ground tissue composed of thin-walled fiber-tracheids (570–)710(–870) μm long with bordered pits most numerous on radial walls, the pits 5–6 μm in diameter, with slitlike apertures extending only slightly beyond pit borders. Spiral and annular thickenings prominent (FIGURE 7). Parenchyma diffuse, diffuse in small aggregates, and rarely scanty paratracheal, in strands of (3 or) 4 to 6 (or 7) cells. Rays heterogeneous II, uniseriate rays ca. 8 per mm, multiseriate rays 3 (or 4) cells wide and ca. 4 per mm, tallest rays up to 0.6 mm high. Sheath cells and crystals absent.

Judging from comparisons of juvenile and mature secondary xylem in other *Ilex* species, one would expect mature wood of *Ilex collina* to have considerably broader rays, somewhat fewer vessels, and somewhat wider and longer axial elements. Qualitative or even major quantitative differences with the above description are unlikely, however.



FIGURES 4–10. 4–7, *Ilex collina:* 4, smooth abaxial cuticle; 5, finely striate cuticle; 6, secondary xylem vessel with helical thickenings; 7, fiber-tracheid with spiral to helical thickenings. 8–10, *Nemopanthus mucronatus:* 8, strongly ridged cuticle with fine wax

Nemopanthus mucronatus

Vegetative anatomy[1]

Material studied.[2] Canada. Nova Scotia: *Gorham 45.1351* (L). U.S.A. Maine: Hancock Co., *Dudley 8031* (L). New Hampshire: *Schweinfurth & Correll 11235* (L). Pennsylvania: Pike Co., *Brumbach 7982* (L); cult. Arbor. Barnes Foundation, Merion, *Fogg s.n.* (L).

Surface view. Glabrous (except in *Schweinfurth & Correll 11235,* which has few short, unicellular hairs on adaxial side of midrib). Cuticle of adaxial surface smooth or faintly to conspicuously striate, that of abaxial surface with conspicuous, rather widely spaced ridges (Figure 8). Epidermal cells of adaxial surface with straight to curved (to undulating) walls, those of abaxial epidermis with curved to strongly undulating walls. Epidermal cell pattern modified over major and most minor veins (cells elongate parallel to venation). Stomata confined to abaxial epidermis, irregularly cyclocytic (Figure 3), sometimes tending to anomocytic or laterocytic with (3 or) 4 to 6 (or 7) subsidiary cells, guard cell pairs (18–)21–25(–30) by (17–)18–21(–26) μm. Peristomal rims present. Cuticular T-pieces absent.

Transverse section. Lamina dorsiventral, 90–190 μm thick. Cuticle usually ca. 1 (rarely up to 2) μm thick. Unspecialized epidermal cells usually flattened, the adaxial cells larger than abaxial, often with convex inner periclinal walls and periclinal wall divisions, only rarely resembling mucilage cells. Hypodermis absent. Mesophyll composed of 1 layer of palisade cells and fairly loose spongy tissue. Midrib very shallowly grooved to raised adaxially, prominently raised abaxially, supplied with single shallowly arc-shaped collateral bundle (sometimes with additional small dorsal bundle) having poorly differentiated abaxial sclerenchyma cap. Ground tissue of midrib collenchymatous. Veins mostly vertically transcurrent through parenchymatous to collenchymatous bundle-sheath extensions, only smallest veins embedded in mesophyll. Petiole with single collateral bundle having incurved margins at basal end (type 2; cf. Baas, 1975) and additional latero-dorsal wing bundles at distal end (type 4). Crystals present as druses, especially in vicinity of vascular bundles.

Wood anatomy

The wood specimens described in Baas (1975), as well as twigs of the herbarium specimens cited above, were examined for presence or absence of spiral thickenings. Such tertiary thickenings were absent from the fiber-tracheids in

[1]An amplified, nearly identical version of the previously published account (Baas, 1975).

[2]In addition to that studied previously, listed in Baas (1973, 1975).

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platelets; 9, secondary xylem vessel without spiral thickenings; 10, detail of vessel tip with very faint wall thickenings.

TABLE 1. **Differences between Ilex collina and Nemopanthus mucronatus.**

CHARACTER	SPECIES	
	Ilex collina	*Nemopanthus mucronatus*
Leaf		
Abaxial cuticle	Smooth or striate	Characteristically ridged
Indumentum	Long, partly septate hairs	Usually absent; if present, hairs short, nonseptate
Stomata	Strongest tendency toward anomocytic	Strongest tendency toward cyclocytic
Average length of guard cell pairs (μm)	26–32	21–25
Midrib	Typically grooved, with poorly developed collenchyma in ground tissue	Usually raised, with well-developed collenchyma in ground tissue
Veins	Mostly embedded and not prominent in epidermal cell pattern	Mostly vertically transcurrent, prominent in epidermal cell pattern
Spiral thickenings in secondary xylem	Prominent in fiber-tracheids and vessels	Typically absent, or very faint and in vessels only

all material studied (see FIGURE 9), although *Dudley 8031* and *Schweinfurth & Correll 11235* showed extremely fine thickenings in some vessel members, especially near the tails (FIGURE 10). No other material studied had any spiral thickening in the vessels (see FIGURE 9).

COMPARISONS AND DISCUSSION

ILEX COLLINA AND NEMOPANTHUS MUCRONATUS

From the above descriptions many similarities in general characters are apparent between the two species. The differences worthy of listing are shown in TABLE 1. Most of them (indumentum, stomatal type and size, midrib and vein characters, spiral thickenings in the wood) are only of interest as diagnostic aids at the species level. However, when these differences are considered together with the more significant one of cuticular sculpturing, they constitute enough evidence to render questionable Clark's (1974) transfer of *Ilex collina* to *Nemopanthus*. Before any decision can be made, it must first be determined whether *Ilex collina* has closer anatomical affinities with other *Ilex* species than with *Nemopanthus mucronatus*.

ILEX COLLINA AND OTHER ILEX SPECIES

The leaf and xylem anatomy of *Ilex collina*, as well as its macromorphological characters and its deciduous habit, are quite similar to those of several species grouped together in subg. PRINUS by Loesener (1942). In fact, in leaf and wood

anatomy a species like *I. decidua* is much more similar than *Nemopanthus mucronatus* to *I. collina*; the only differences are in some minute details of the indumentum and in the outline of the abaxial epidermal cells. I also studied two specimens labeled *I. longipes* Chapman in the Rijksherbarium (U.S.A.: Massachusetts, cult. *Arnold Arboretum 22659* (*Boom 39981*); Tennessee, *Biltmore Herb. 4063*). Apparently these specimens are not *I. collina* because their indumentum is different (short, unicellular hairs instead of long ones; see also description in Baas, 1975). They also differ from the *I. decidua* specimen that I studied (1975); this might have been expected considering Clark's remark that *I. longipes* sensu Trelease in fact belongs to the *I. decidua* complex. Apparently identifications on herbarium labels in this group of *Ilex* species are far from reliable, and I therefore refrain from earmarking a particular *Ilex* species as being anatomically closest to *I. collina*. For the present problem, it is significant only that several species of subg. PRINUS "ser. B" PRINOIDES anatomically resemble *I. collina* more closely than *I. collina* resembles *Nemopanthus mucronatus*. *Ilex serrata* Thunb. and *I. verticillata* (L.) A. Gray of "ser. A" EUPRINUS (*sensu* Loesener) (= PRINUS) also resemble *I. collina* in leaf anatomy but differ markedly in their wood anatomy because they lack spiral thickenings in the fibers and vessels.

NEMOPANTHUS MUCRONATUS AND ILEX

As stated before, the only constant anatomical difference between *Ilex* and *Nemopanthus mucronatus* is the sculpturing of the abaxial cuticle. Within *Ilex* (especially in some tropical species) sculpturing ranges from smooth to conspicuously striate, but it is nowhere near as marked as in *Nemopanthus*. Another distinguishing character of *N. mucronatus* is its lack of conspicuous spiral thickenings, which are typical for all *Ilex* species studied from temperate regions except *I. serrata* and *I. verticillata*. It is clear that although cuticular sculpturing is of considerable diagnostic value, it alone cannot justify the separation of two obviously closely related genera. All characters must be examined to determine whether other differences are sufficient to maintain *Nemopanthus* as a separate genus.

SUGGESTIONS FOR TAXONOMIC TREATMENT

Ilex collina is anatomically much closer to several *Ilex* species belonging to "ser. B" PRINOIDES of subg. PRINUS than it is to *Nemopanthus mucronatus*. Translated into taxonomic practice, this would favor the reinstatement of *Nemopanthus collinus* in *Ilex*, in contrast to Clark's (1974) treatment of the species.

Nemopanthus mucronatus shows anatomical affinities to several *Ilex* species of "ser. A" EUPRINUS rather than to those of "ser. B" PRINOIDES *sensu* Loesener. If it is true that the floral characters of *I. collina* break down the boundaries between *Ilex* and *Nemopanthus*, this implies that *N. mucronatus* should be transferred to *Ilex* and should in the future be treated as *Ilex mucronata*. However, if floral and other macromorphological distinctions remain, the additional differences in cuticular structure can be used in support of maintaining *Nemopanthus* as a monotypic genus.

ACKNOWLEDGMENTS

I am greatly indebted to Theodore Dudley and Gene Eisenbeiss (U. S. National Arboretum, Washington, D. C.) for the generous supply of research material and for drawing my attention to this interesting problem. I also thank Paul van Veen for preparing numerous anatomical slides of troublesome herbarium material.

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THE CHROMOSOMES AND RELATIONSHIPS OF METASEQUOIA AND SEQUOIA (TAXODIACEAE): AN UPDATE[1]

S. E. SCHLARBAUM, T. TSUCHIYA, AND L. C. JOHNSON

IN 1948 Stebbins reported on the chromosome number and relationships of the newly discovered *Metasequoia glyptostroboides* Hu & Cheng ($2n = 2x = 22$) and *Sequoia sempervirens* (D. Don) Endl. ($2n = 6x = 66$). Further research on the karyological relationships between these two taxodiaceous species has not been reported in the following years. The observation of marker chromosomes with unusual structures in various species of Taxodiaceae (Schlarbaum & Tsuchiya, 1975, 1976, 1981) stimulated the authors to investigate the chromosome morphology of *Metasequoia* and *Sequoia* for possible indications of cytotaxonomic and evolutionary relationships. This paper is a brief report addressing only the marker chromosome differences between *Metasequoia* and *Sequoia*. Expanded accounts of the overall karyotypic features of these species will be published elsewhere (Schlarbaum & Tsuchiya, 1984; Schlarbaum *et al.*, 1983).

Interest in the chromosome complement of *Sequoia* developed after Lawson (1904) suspected that the species was polyploid. The chromosome number of *Sequoia* was determined with certainty by the independent meiotic studies of Hirayoshi and Nakamura (1943) and Stebbins (1948). FIGURE 1 is the previously unpublished photo by Hirayoshi and Nakamura (both now deceased) showing the chromosome configurations from which the hexaploid count was determined. As shown by this photograph and the drawings of microsporocytes by Stebbins (1948) and Hirayoshi and Nakamura (1943), multivalents are present, suggesting that *Sequoia* is at least partially autopolyploid.

Before the discovery of *Metasequoia* was published, some scientists (Jensen & Levan, 1941; Hirayoshi & Nakamura, 1943) speculated whether *Sequoiadendron giganteum* (Lindley) Buchholz, previously classified as *Sequoia gigantea* (Lindley) Decne., may have contributed one or more genomes to *Sequoia*. The discovery of living *Metasequoia* trees naturally stimulated hypotheses involving ancestral relationships between *Metasequoia* and *Sequoia*. These inferences were based upon the morphological similarities between the two species, and probably in part on the previous confusion of fossil remains of *Sequoia* and *Metasequoia* (Miki, 1941; Chaney, 1951). After determining the diploid nature of *Metasequoia*, Stebbins (1948) considered the plausibility

[1]Contribution from the Department of Agronomy, Colorado State University. Published with the approval of the Director of the Colorado State Experiment Station as Scientific Series paper no. 2769.

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FIGURE 1. Microsporocyte of *Sequoia sempervirens* showing complete chromosome complement ($2n = 2x = 66$) and various multivalents, × ca. 2200 (Hirayoshi & Nakamura, unpubl.).

of a *Metasequoia* species being a Mesozoic or early Tertiary ancestor of *Sequoia*. More recently, Saylor and Simons (1970) speculated on the possibility of chromosomal relationships between *Metasequoia* and *Sequoia*.

In the present study, observations for marker chromosomes were made on the root-tip mitosis of *Sequoia* and *Metasequoia*. *Sequoia* seeds from an unknown locality were obtained from a commercial company and germinated. *Metasequoia* cuttings were taken from trees originating from the only extant population in western Hubei Province, China, and rooted. Cytological methodology followed Schlarbaum and Tsuchiya (1976). Vouchers are deposited at CS.

Our karyological observations show the presence of marker chromosomes with unusual structures in *Metasequoia* and *Sequoia* (FIGURE 2, a, b). *Metasequoia* has three pairs of chromosomes with long kinetochore regions (FIGURE 2, a). *Sequoia* has two pairs of SAT-chromosomes with long secondary constrictions in which chromomeres are visible, and another chromosome pair that probably has microsatellites attached to the short arm (Schlarbaum, 1980; Schlarbaum & Tsuchiya, 1984) (FIGURE 2, b; microsatellites not visible).

FIGURE 2. Marker chromosome pairs, × 3000: a, *Metasequoia glyptostroboides*, $2n = 2x = 22$, showing long kinetochore regions; b, *Sequoia sempervirens*, $2n = 6x = 66$ (left and center pairs show long secondary constrictions and corresponding satellite bodies).

CONCLUSIONS

The marker chromosome type found in *Metasequoia* was not observed in *Sequoia*, indicating the lack of a direct cytotaxonomic relationship between the two species, although the effects of amphiplasty (Navashin, 1928) cannot be entirely discounted. Based on the cytological evidence presented, genomic contribution of the extant *Metasequoia* species to the polyploidy of *Sequoia* is considered unlikely. It must be recognized that the chromosome studies were conducted on monotypic, relictual genera that undoubtedly contained more species in past geologic epochs. However, the fossil record supports the cytological conclusion that *Sequoia* was differentiated independently from *Metasequoia* but probably came from the same general ancestral stock (Arnold & Lowther, 1955).

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BERNICE G. SCHUBERT (photograph taken in 1974).

It is with respect and affection that the staff of the Arnold Arboretum dedicates this number of the *Journal of the Arnold Arboretum* to Bernice G. Schubert, Curator of the Arnold Arboretum and Senior Lecturer on Biology in the Faculty of Arts and Sciences of Harvard University. Dr. Schubert retired from the staff of the Arnold Arboretum at the end of June, following her seventieth birthday. We are joined by her many friends and colleagues both here at Harvard and around the world in wishing her continued good health and many happy years ahead.

Dr. Schubert came to the Gray Herbarium of Harvard University in 1935 to pursue her graduate education, and she received the Ph.D. degree from Radcliffe College in 1941. Her thesis research centered on the leguminous genus *Desmodium,* and the genus has remained one of her primary research interests to the present day. As a result of her studies, she has contributed treatments of *Desmodium* for numerous regional floras of the United States, Mexico, Central and South America, Africa, and Asia. During the early 1940's, her interest was also aroused in the New World species of *Begonia,* and several of her important contributions to the taxonomy of the genus have been completed in collaboration with her friend and colleague, Lyman Smith.

After the completion of her graduate training, Dr. Schubert remained at the Gray Herbarium until 1950 as assistant to the Director, Professor M. L. Fernald, who was then completing the eighth edition of Gray's *Manual of Botany.* For this work Dr. Schubert traveled to Europe in 1946–47 to photograph type specimens in several European herbaria. Her photographs appear in many of Professor Fernald's papers published in *Rhodora* and the *Contributions from the Gray Herbarium* and also in the ten papers they published together. In the final stages of production of the eighth edition of Gray's *Manual,* Dr. Schubert saw the book through publication and was, in fact, Fernald's "eyes" for this critical job. Fernald wrote in his acknowledgments, "Finally, especially since the impairment of his eyesight, the author has had the most loyal, conscientious and unlimited aid of Dr. Schubert in the exacting details of coordinating usages in the text, editing the manuscript for the printer, checking and double-checking the citations of figures and the scores of other details necessary in the book as it goes to press. My appreciation of all her helpfulness can not be adequately expressed. Cambridge, June 1949."

In 1950 Dr. Schubert was awarded a Guggenheim Fellowship for study in Europe, and during 1951 and 1952 she remained in Belgium, where she worked on a cooperative project involving the floras of Africa, especially that of the Belgian Congo (Zaire). She returned to the United States in 1952 to work with the New Crops Research Branch of the U. S. Department of Agriculture. It was during this period that she initiated her studies of the taxonomically com-

plex genus *Dioscorea,* the true yams and the group that completes the triad of genera for which she is well known. It was also while she was at the U.S.D.A. that she published with the late J. J. Willaman the fundamental reference, *Alkaloid-Bearing Plants and Their Contained Alkaloids.*

Bernice rejoined the Harvard botanical community in 1962 when she returned to Cambridge as a curator of the Arnold Arboretum and as editor of the *Journal of the Arnold Arboretum.* She filled the latter role from 1963 to 1979, maintaining the *Journal* as one of the best-edited botanical periodicals of its kind. In this work her kind consideration for authors was unusual, and many of the contributing authors during her term as editor are only too well aware of the debt they owe to her for the improvement of their manuscripts. She was particularly generous in the time and work she was willing to expend on manuscripts received from graduate students, from authors with newly won Ph.D.'s, and from foreign botanists whose English required polishing. In 1979 she assumed chairmanship of the newly established Arnold Arboretum Publications Committee, a post she held until her retirement.

Dr. Schubert served as supervisor of the Harvard University Herbaria building from 1969 through 1975, an often thankless position requiring constant attention to the maintenance and day-to-day operation of the herbaria building. She was also appointed Senior Lecturer in the Department of Biology and in this capacity advised numerous undergraduate biology majors and worked closely with graduate students in botany. Over the years Bernice has been unfailing in her encouragement of young botanists; she has helped countless correspondents, including many from Mexico and Central and South America, and numerous amateurs with a deep interest in the genus *Begonia.*

Throughout her career Dr. Schubert has visited Mexico and Central and South American countries to collect specimens for her studies and to participate in botanical activities at several universities and research stations. She has also been a regular participant in Mexican botanical congresses, and she has been named honorary vice president of several of these congresses in recognition of her contributions to Mexican botany and her encouragement and help to young botanists. She was further honored with a vice presidency of the III Congreso Latinoamericano y II Nacional (Peruano) de Botánica in Lima in 1982. We expect that she may wish to escape winter weather in Massachusetts through continued visits "south of the border," but we are hopeful that her taxonomic and curatorial work, as well as her editorial advice, will continue at the Harvard University Herbaria.

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A TAXONOMIC REVISION OF THE AMERICAN SPECIES OF AGARISTA (ERICACEAE)[1, 2]

WALTER S. JUDD

A GENUS of 30 species occurring in both Africa (including Madagascar) and the Americas, *Agarista* is closely related to several genera in the Andromedeae (Ericaceae) such as *Craibiodendron* W. W. Smith, *Lyonia* Nutt., and *Pieris* D. Don (see Stevens, 1970, 1971; Judd, 1979). In this paper I have reevaluated the limits of the genus and revised the species occurring in the New World; ca. 1900 herbarium specimens have been examined. Usually the African taxa are treated as the genus *Agauria,* and the American species as a section of the eastern Asian–North American genus *Leucothoë* D. Don (see Sleumer, 1938, 1959). The interrelationships and confused taxonomic history of these three groups have been studied by Stevens (1970) and Judd (1979) and are reinvestigated here.

The American species of *Agarista* form a very homogeneous and obviously closely related group, and it has been difficult to delimit phylogenetic groupings of species within this section. However, the taxonomic usefulness of many characters employed in species delimitation (e.g., presence of unicellular hairs and multicellular gland-headed hairs, inflorescence structure, leaf shape) has been reevaluated. I have attempted to employ consistent specific concepts, to compare the taxa and interpret their evolutionary relationships, and to develop practical keys for identification.

PHYLOGENY AND EVOLUTION

GENERIC AND SECTIONAL RELATIONSHIPS

The genus *Agarista* can be divided into two natural and morphologically distinctive groups that are recognized in this treatment as sections. *Agarista*

[1]The third in a series of revisionary studies of genera of the Andromedeae (Ericaceae). Previously studied genera include *Lyonia* (Judd, 1981) and *Pieris* (Judd, 1982).

[2]Florida Agriculture Experiment Station Journal Series no. 4262.

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sect. AGAURIA includes the single widespread and variable species *A. salicifolia*, which is native to central Africa and Madagascar (see Sleumer, 1938). This taxon is characterized by twigs with nonchambered, slightly to very heterogeneous pith; leaves with the abaxial epidermis papillose and the adaxial epidermis having more or less short, usually undivided cells (in cross section); and capsules with basal placentae. In addition, the style is apparently not swollen. *Agarista* sect. AGARISTA includes 29 species (34 taxa) and is most diverse in South America, especially southeastern Brazil. These species are characterized by twigs with non- to clearly chambered, *Calluna*-type pith (i.e., cells small and thick walled toward the outside of the twig, becoming much larger and thinner in the center); leaves with the abaxial epidermis nonpapillose and the adaxial epidermis with usually tall and often divided cells; and capsules with subapical to more or less central placentae. The style is usually swollen toward the apex.

Stevens (1970) has pointed out that the African and American taxa also differ in the development of a hypodermis. *Agarista salicifolia* has a more or less continuous hypodermis, while the American species have at most one or two cells (in cross section) near the larger veins. Additionally, Cox (1948) has reported differences in the anatomy of the xylem.

The sections are very similar in most features. Both are characterized by buds with more than two bud scales; an indumentum of multicellular, multiseriate-stalked, small-headed glandular hairs; leaves usually revolute in bud, with a unifacial midrib bundle and a rather dense vein reticulum in which all orders are more or less equally prominent (Lems, 1964); inflorescences racemose (or paniculate), overwintering within the bud (Lems, 1962); flowers five-merous, with imbricate calyx lobes; stamens lacking appendages, the filaments geniculate (i.e., S-shaped) and with usually long unicellular hairs; and capsules with nonthickened sutures.

Traditionally, *Agarista salicifolia* has almost always been included in the genus *Agauria* (see TABLE 1) and the American species of *Agarista* in *Leucothoë* sect. AGASTIA (see TABLE 1; Sleumer, 1959). However, these two groups are actually very similar phenetically and cladistically and are obviously closely related; neither is close to *Leucothoë* sensu stricto (TABLE 2; Lems, 1964; Stevens, 1970; Judd, 1979). All the characters by which these two sections differ (e.g., pith type, presence of papillae on the abaxial leaf epidermis, placenta position, and presence of a leaf hypodermis) are variable infragenerically—and also sometimes infraspecifically—in at least one closely related genus (*Pieris*, *Lyonia*, or *Craibiodendron*). In addition, the degree of morphological/anatomical divergence between *Agarista salicifolia* and the American species of *Agarista* is comparable to that separating sections within other genera of the Andromedeae (see TABLE 2; Judd, 1969, *fig. 1*), while their differences with *Leucothoë* are of "generic magnitude" (TABLE 2; Judd, 1979). The African and American species also form a monophyletic group (see Judd, 1979, *fig. 2*) based upon the shared derived characters of densely reticulate-veined leaves that are usually revolute in bud. This group is part of a larger monophyletic group that includes *Lyonia*, *Craibiodendron*, and *Pieris* and is characterized by anomocytic stomata, fiber bands in the phloem, usually elongated seed-coat cells,

TABLE 1. **Comparative treatment of Agarista and Leucothoë by various authors.**

AUTHOR	TAXON		
	Agarista sect. **Agarista**	**Agarista** sect. **Agauria**	**Leucothoë** (several sections)
Lamarck (1783)	*Andromeda*	*Andromeda*	*Andromeda*
Michaux (1803), Nuttall (1818)	*Andromeda*	—	*Andromeda*
G. Don (1834)	*Agarista* (but *A. populifolia* placed in *Leucothoë*)	*Agarista*	*Leucothoë*
De Candolle (1839)	*Leucothoë* sect. *Agastia* (but 2 spp. placed in *Amechania*, 2 in *Leucothoë* sect. *Agauria*, 1 in *Leucothoë* sect. *Euleucothoë*)	*Leucothoë* sect. *Agauria*	*Leucothoë* sect. *Euleucothoë* (but 1 sp. placed in *Zenobia*)
Bentham & Hooker (1876)	*Agarista* (but *A. populifolia* placed in *Leucothoë* sect. *Euleucothoë*)	*Agauria*	*Leucothoë* (2 sections)
Gray (1878)	*Leucothoë*	*Agauria*	*Leucothoë* (2 subgenera treated)
Niedenzu (1889)	*Agarista* (2 sections, *A. populifolia* placed in *Leucothoë* sect. *Euleucothoë*)	*Agauria*	*Leucothoë* (2 sections)
Drude (1897)	*Leucothoë* subg. *Agarista* (but *A. populifolia* placed in subg. *Euleucothoë*)	*Agauria*	*Leucothoë* subg. *Euleucothoë* and *Lyonia* subg. *Eubotrys*
Small (1914)	*Leucothoë* (only *A. populifolia* treated)	—	*Eubotrys*, *Leucothoë*, *Oreocallis* (but E Asian spp. not treated)
Sleumer (1938, 1959)	*Leucothoë* sect. *Agastia*	*Agauria*	*Leucothoë* (6 sections)
Stevens (1970, 1971)	*Agarista*	*Agauria*	*Leucothoë*

geniculate and/or spurred filaments, and tendency toward epidermal lignification.

The various generic and infrageneric classifications of the species here considered in *Agarista* are summarized in TABLE 1 (see also Stevens, 1970; Judd, 1979). The generic delimitation adopted here is essentially that of G. Don (1834). Lamarck (1783) described—as species of the then very broadly defined

TABLE 2. **Variation in selected morphological and anatomical characters in Agarista and Leucothoë.**

CHARACTER	TAXON		
	Agarista sect. **Agarista**	**Agarista** sect. **Agauria**	**Leucothoë**
Wood			
Phloem with bands of fibers	+	+	−
Pith	*Calluna*-type (often septate)	Slightly to very heterogeneous	Variable
Plant evergreen	+	+	+/−
Leaves			
Revolute in bud	+(−)	+	−
Margin serrate	−(+)	−	+
Vein reticulum dense	+	+	−
Epidermis lignified	+	+	−
Epidermal cells divided	+(−)	−(+)	−
Abaxial epidermis papillose	−	+	−
Stomata anomocytic	+	+	−
Anthers			
Filaments geniculate	+	+	−
Filaments with unicellular hairs	+	+	+/−
Awns present	−	−	+(−)
Placenta position	Apical (central)	Basal	Apical
Testa cells	Elongated	Elongated	± Isodiametric
Number of species	29	1	8

genus *Andromeda*—the first known species of both sections of *Agarista*: *A. populifolia* of sect. AGARISTA, and *A. salicifolia* of sect. AGAURIA. Important nineteenth-century treatments of the group include those of G. Don (1834), De Candolle (1839), Meissner (1863), and Bentham and Hooker (1876). More recently, Sleumer (1938, 1959) has extensively studied both the African and the American taxa, and Kinoshita-Gouvêa (1980) has included the Brazilian species as part of her floristic study of the Ericaceae of Brazil. Stevens (1970) was the first contemporary botanist to reaffirm the close relationship between the African and American agaristas.

CLADISTIC ANALYSIS

The phylogenetic relationships of the species of *Agarista* sect. AGARISTA were investigated using the method of Wagner (1961, 1962, 1969, 1980). Twenty-seven characters were used and assigned primitive and advanced states. Most of these characters are quantitative, and the states of such characters are necessarily somewhat arbitrarily defined. However, the dividing point of character states was chosen in such a way as to minimize the number of taxa showing

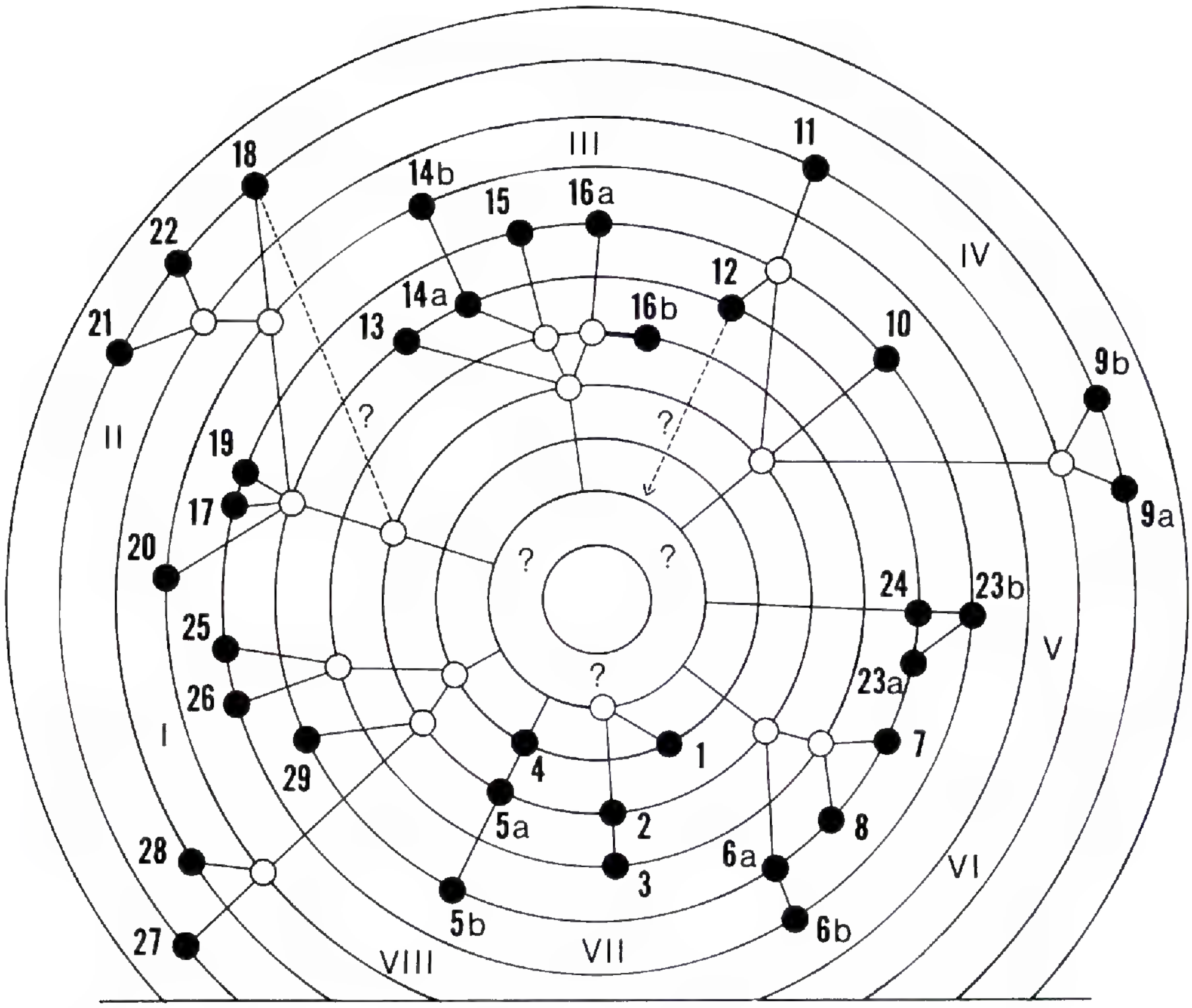


FIGURE 1. Wagner tree for species and varieties of *Agarista* sect. AGARISTA: extant taxa (black circles); hypothetical ancestors showing only derived character states shared by taxa positioned distally on tree (open circles). Taxa indicated by numerals assigned in taxonomic treatment: I = *Agarista eucalyptoides* group, II = *A. hispidula* group, III = *A. oleifolia* group, IV = *A. coriifolia* group, V = *A. niederleinii* group, VI = *A. populifolia* group, VII = *A. albiflora* group, VIII = *A. revoluta* group. (See TABLE 4 for derived character states for each species or variety, and for distinctive features of each species group.)

both conditions. TABLE 3 lists these characters. For each of them, a taxon was scored 0 if primitive and 1 if advanced. When two or more states of a given character were considered derived, each was given a lower-case alphabetic superscript (e.g., 1^a, 1^b). TABLE 4 shows all taxa and their character-state values. For each taxon the total divergence index was determined by adding the individual character-state values. Then mutual groupings of derived characters were determined (by hand), and the taxa were arranged in sequence according to these groupings. In the process, an attempt was made to minimize the number of character-state reversals and parallelisms. The taxa were then plotted graphically (FIGURE 1), with the branching points determined by the mutual grouping of derived characters and the distance by the divergence of each taxon.

The Wagner Groundplan Divergence method, like other cladistic methods,

TABLE 3. **Characters used in the phylogenetic study of the species and varieties of Agarista sect. Agarista.**

CODE	CHARACTER	PRIMITIVE STATE	ADVANCED STATE
A	Habit	± Well-branched shrubs or trees	Subshrubs with rigidly ascending branches
B	Gland-headed hairs	At least sometimes present	Lacking
C	Stem glaucousness	Lacking	At least sometimes present
D	Pith (degree of septation)	Nonseptate to irregularly septate	At least sometimes clearly septate
E	Pith (cellular structure)	Homogeneous	*Calluna*-type
F	Leaf size	Usually > 3 cm	Usually < 2.5 cm
G	Leaf shape	Usually ± ovate to elliptic	a. Often oblong b. ± Linear c. Often ± orbicular
H	Leaf apex	Acute to rounded-mucronate	a. Often acuminate b. Consistently rounded- to retuse-mucronate
I	Leaf base	Not cordate	At least sometimes cordate
J	Abaxial laminar glands	± Lacking or inconspicuous	At least sometimes conspicuous
K	Unicellular hairs on abaxial leaf surface	Lacking to sparse	Usually ± dense
L	Lamina	± Flat to very slightly revolute at margin	a. Slightly to strongly adaxially folded b. Often with strongly revolute margin c. Often clearly curved toward abaxial surface
M	Lamina texture	Coriaceous, ± flexible when dry	Very coriaceous, ± inflexible when dry
N	Leaf margin	Entire (mature leaves)	a. Often crisped/undulate b. Often serrate
O	Petiole length	Short to moderate	Often elongate
P	Inflorescence position	Axillary	Axillary or sometimes terminal
Q	Inflorescence type	Raceme	a. Raceme or panicle b. Sometimes flowers solitary
R	Inflorescence length	> 3 cm	< 3 cm
S	Inflorescence indumentum (unicellular)	Hairs (short, whitish) often present	a. Nearly always lacking b. Hairs ferrugineous c. Hairs long, whitish
T	Calyx lobe length	Usually < 3 mm	Usually > 3 mm
U	Corolla color	White, to pink tinged at apex	Often red

TABLE 3 (*continued*).

CODE	CHARACTER	PRIMITIVE STATE	ADVANCED STATE
V	Corolla size	< 13 mm	Often > 13 mm
W	Corolla pubescence (abaxial surface)	Lacking (or very sparse)	Sparse to dense
X	Ovary pubescence (unicellular)	At least a few hairs	Lacking
Y	Placenta position	± Subapical	± Central
Z	Capsule wall	Not stout	Stout
AA	Seed length	Usually ≥ 2 mm	Usually < 1.5 mm

requires numerous assumptions concerning which is the derived and which the ancestral state of each character. The problems and sources of error associated with each step in the procedure are discussed in Judd (1979), Stevens (1980, 1981), Crisci and Stuessy (1980), Wiley (1981), Watrous and Wheeler (1981), and Wheeler (1981). Although the consensus is that out-group analysis is the most powerful method for determining polarity, Crisci and Stuessy maintain that in-group analysis, if used with care, can be helpful in phylogenetic investigations. The derived state(s) of characters A–G, I–L, N–P, T, U, W, and Y were determined by out-group comparison (using the genera *Craibiodendron* and *Lyonia* as the outgroup; see Judd, 1979), supported by in-group comparison for the character states A, C, F, G, J–L, N–P, T, U, W, and Y. Characters AA and Y are highly correlated. In-group comparison was used in determining the advanced state(s) of H, M, Q–S, V, X, and Z. These decisions were made after careful study of the genus and related groups.

The Wagner Tree resulting from the above procedure (FIGURE 1; see also TABLE 4) indicates that the species of *Agarista* sect. AGARISTA may belong to eight clearly to rather poorly defined phyletic groups: the *Agarista eucalyptoides* group (species 25–29), the *A. hispidula* group (species 17–22), the *A. oleifolia* group (species 13–16), the *A. coriifolia* group (species 9–12), the *A. niederleinii* group (species 23, 24), the *A. populifolia* group (species 6–8), the *A. albiflora* group (species 1–3), and the *A. revoluta* group (species 4, 5). It is also evident that the most advanced taxa—*Agarista coriifolia, A. angustissima, A. glaberrima, A. virgata, A. hispidula,* and *A. ericoides*—are all indigenous to southern Brazil. Most are, in fact, endemic or nearly endemic to Minas Gerais. In contrast, the more primitive taxa—*Agarista albiflora, A. subcordata,* and *A. duckei*—are found in northern South America, the two former in the northern Andes and the latter in the Guayana Highland.

The species of the *Agarista eucalyptoides* group are characterized by their distinctive leaves with often elongate, flexuous petioles (O) and acuminate apices (H^a). These species also have leaves with rounded to narrowly cuneate bases, white flowers with short calyx lobes, and capsules with subapical placentae. *Agarista eucalyptoides* and *A. boliviensis* are likely closely related. Both taxa lack gland-headed hairs (B), have often crisped/undulate leaf margins (N^a), and have leaves that are revolute in bud and more or less flat at maturity. In contrast, the more advanced *A. duartei, A. angustissima,* and *A. glaberrima*

TABLE 4. **Character divergence values for taxa used to construct Wagner Tree.**

Taxon	Character A B C D E F G H I J K L M N O P Q R S T U V W X Y Z AA	Geog.	Total
1	0 0 0 0 1 0 0 0 | 1 | 0 0 0 0 0 0 0 0 0 0 1c0 0 0 0 0 0 0 0 0	A	3
2	0 1 0 0 1 1 0 0 | 1 | 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 ?	A	4
3	0 1 0 0 1 1 0 0 | 0 | 0 0 1b0 0 0 0 0 0 0 0 0 0 0 1 0 0 0	A	5
4	0 | 1 | 0 0 1 0 0 0 0 0 0 | 1c0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	G	3
5a	0 | 1 | 0 0 1 0 0 1b0 0 0 | 1c0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	B-N	4
5b	0 | 1 | 0 0 1 0 0 1b0 0 1 | 1c0 0 0 0 0 0 0 0 0 0 1 0 0 ? ?	B-N	6
6a	0 | 1 | 0 | 1 | 1 0 0 | 1a0 0 0 0 0 0 0 0 0 | 1 | 0 0 0 0 1 0 0 0 0	NA	6
6b	0 | 1 | 0 | 1 | 1 0 0 | 1a0 0 1 0 0 0 0 0 0 | 1 | 0 0 0 0 1 0 0 0 0	NA	7
7	0 | 1 | 0 | 1 | 1 0 0 | 1a0 0 0 0 0 0 0 0 0 | 1 | 0 0 0 0 0 1 0 0 0	NA	6
8	0 | 0 | 0 | 1 | 1 0 0 | 1a0 0 0 0 0 1b0 0 0 | 1 | 0 0 0 0 0 1 0 0 0	NA	6
9a	0 | 1 | 1 1 1 0 0 0 1 | 1 | 0 0 | 1 | 0 0 1 1a0 0 0 1 0 0 0 0 0 0	B-N	10
9b	0?| 1 | 1 1 1 0 1a0 0 | 1 | 0 0 | 1 | 0 0 1 1a0 0 0 1 0 0 0 0 0 0	B-N	10
10	0 | 1 | 0 0 1 1 0 0 1 | 1 | 0 0 | 1 | 0 0 0 0 0 0 0 0 0 0 0 0 0 1	B-N	7
11	0 | 0 | 0 0 1 1 0 0 1 | 1 | 1 0 | 1 | 0 0 0 0 0 1c0 1 0 1 0 0 0 0?	B-N	9
12	0 | 1 | 0 0 1 0 1a0 0 | 0 | 1 0 | 0 | 0 0 0 0 0 1c0 0 0 1 0 0 0 0	B-N	6
13	0 0 0 0 1 0 0 0 | 1 | 0 1 0 0 0 0 0 0 0 0 0 | 0 | 0 1 0 | 1 | 0 | 1	B-S	6
14a	0 0 0 1 1 0 0 0 | 1 | 0 0 0 0 0 0 0 0 0 0 0 0 | 1 | 0 0 0 | 1 | 0 | 1	B-N	6
14b	0 0 0 1 1 0 0 0 | 0 | 0 0 0 0 0 0 0 0 0 0 1a0 | 1 | 1 0 1 | 1 | 0 | 1	B-N	8
15	0 1 0 1 1 0 1 0 | 0 | 0 0 0 0 0 0 0 0 0 1 0 0 | 0 | 0 0 0 | 1 | 0 | 1	B-S	7
16a	0 0 0 0 1 0 0 0 | 1 | 0 0 0 0 0 0 0 1 1a0 0 0 | 1 | 0 0 0 | 1 | 0 | 1	B-S	7
16b	0 0 0 0 1 1 0 0 | 1 | 0 0 0 0 0 0 0 0 0 0 0 0 | 1 | 0 0 0 | 0 | 0 | 1	B-N	5
17	1 | 0 0 0 1 1 1c1b1 | 0 0 0 | 0 0 0 0 0 0 0 0 | 1 | 0 0 0 0 0 0 0 0	B-S	7
18	1 | 0 0 0 1 1 0 0 | 1 | 0 0 | 0 0 0 0 1 1a0 | 1 | 0 0 0 0 1 1 0 1	B-N	10
19	1 | 0 0 0 1 1 0 0 | 1 | 0 0 | 1b0 0 0 1 0 0 0 | 1 | 0 0 0 0 0 0 0 0	B-NS	7
20	0?| 1 0 1 1 1 0 0 | 1 | 0 0 | 1b0 0 0 0 1b1 0 0 | 0 0 0 0 0 0 0 0	B-N	8
21	1 | 0 0 0 1 1 0 0 | 1 | 0 0 | 1b0 0 0 0 0 0 0 | 1 | 1 0 1 0 1 0 1	B-N	10
22	1 | 0 0 0 1 1 0 0 | 1 | 0 0 | 1b0 0 0 0 0 1 0 | 1 | 1 0 0 0 1 0 1	B-N	10
23a	0 | 1 | 0 | 1 | 1 1 1 0 0 0 0 0 0 0 0 0 0 | 0 | 0 0 0 0 0 0 0 | 1 | 0	B-S	6
23b	0 | 1 | 0 | 1 | 1 0 1 1a0 0 0 0 0 0 0 0 0 | 1 | 0 0 0 0 0 0 0 | 1 | 0	B-S	7
24	0 | 1 | 0 | 1 | 1 0 0 1a0 0 0 0 0 0 0 0 0 | 1 | 0 0 0 0 0 0 0 | 1 | 0	B-N	6
25	0 1 0 0 1 0 0 | 1a0 0 0 | 0 | 0 1a1 | 0 0 1 0 0 0 0 0 1 0 0 0	A	7
26	0 1 0 0 1 0 1a| 1a0 0 0 | 0 | 0 1a1 | 0 0 0 1b0 0 0 0 0 0 0 0	B-NS	7
27	0 1 0 1 1 0 0 | 1a0 0 0 | 1a0 0 | 1 | 1 1a0 1a0 0 0 0 1 0 0 0	B-N	10
28	0 0 0 0 1 0 1b| 1a0 0 0 | 1a0 0 | 1 | 1 1a0 1a0 0 0 0 1 0 0 0	B-N	9
29	1 0 0 0 1 0 1b| 1a0 0 0 | 1a0 0 | 0 | 0 0 1 0 0 0 0 0 0 0 0 0	B-N	6

Explanation of abbreviations: A = Andes, B = Brazilian region (north and south), G = Guayana Highland, NA = North America. Dotted lines separate species groups supported by characters enclosed within rectangular markings. Each taxon indicated by its species number.

have leaf blades that are slightly to strongly adaxially folded. The distinctive linear leaves (G^b) of *A. angustissima* and *A. duartei* have probably evolved convergently. Except for *A. boliviensis,* which occurs in the southern Andes, all species of this phyletic group are limited to the Brazilian region (see geographic analysis). The group is most diverse in Minas Gerais, with only the relatively widespread *A. eucalyptoides* extending southward into the state of Rio Grande do Sul and adjacent Uruguay.

The species of the *Agarista hispidula* group are characterized by their low, more or less sparsely and erectly branched habit (A) and their small, usually cordate-based leaves (F, I). Many species also have strongly revolute leaves (L^b) and elongate calyx lobes (T). The position of the placenta varies from more or less subapical to central, and the group may be derived from extinct, small-leaved members of the *A. oleifolia* group, an assemblage with mainly central placentae (note especially the resemblance in leaf characters to *A. pulchella* var. *cordifolia*). Although *A. hispidula* and *A. ericoides* are probably closely related, both often having red corollas, more or less centrally positioned placentae, and short seeds, the relationships between these species and *A. chlorantha, A. organensis, A. nummularia,* and *A. virgata* are somewhat obscure. Species of the *A. hispidula* group are limited to the Brazilian region. The group is most diverse in the northern subunit of this region, with only *A. chlorantha* and *A. nummularia* occurring as far south as Santa Catarina (the former) or Rio Grande do Sul (the latter).

The *Agarista oleifolia* group is a rather loosely knit assemblage of taxa characterized by often cordate-based leaves (I), and by capsules with central placentae and short seeds (Y, AA). These species tend to have more or less flat leaves and flowers with short calyx lobes. Several taxa have straight-sided or oblong leaves (G^a). The relationships between the taxa comprising this rather weakly defined group are obscure. The group is limited to the Brazilian region (including Paraguay).

The four species of the *Agarista coriifolia* group are characterized by their lack of multicellular gland-headed hairs (B), and by their usually quite coriaceous leaves (M) with often conspicuous abaxial glandular regions along the midvein (J). The leaves tend to be more or less flat, the inflorescences elongate, and the placentae subapical. The calyx lobes are usually short, and the flowers tend to be reddish. The affinities of *A. chapadensis* are probably with *A. subrotunda,* a species with moderately to densely pubescent abaxial leaf and corolla surfaces (K, W). The species of this evolutionary line are limited to the northern portion of the Brazilian region (see phytogeographic discussion).

The *Agarista niederleinii* group includes only three taxa, which are distinguished by their lack of multicellular gland-headed hairs (B), their often septate pith (D), and their large capsules with very stout walls (Z). These taxa also tend to have short racemes (R), subapically positioned placentae, white flowers with short calyx lobes, and flat to slightly revolute leaves. The group is limited to the Brazilian region.

The *Agarista populifolia* group is distinctive due to its often clearly septate

pith (D), its ovate, acuminate leaves (H^a), and its short racemes (R). The members of this lineage frequently have rather large, more or less flat leaf blades with cuneate to rounded bases, white flowers with short calyx lobes, and capsules with subapical placentae. These species are limited to North and Central America, growing in the southeastern United States and east-central Mexico south to Honduras and El Salvador. This group may have originated from extinct members similar to species of the *A. albiflora* group (note especially the resemblance of leaves to those of *A. albiflora*).

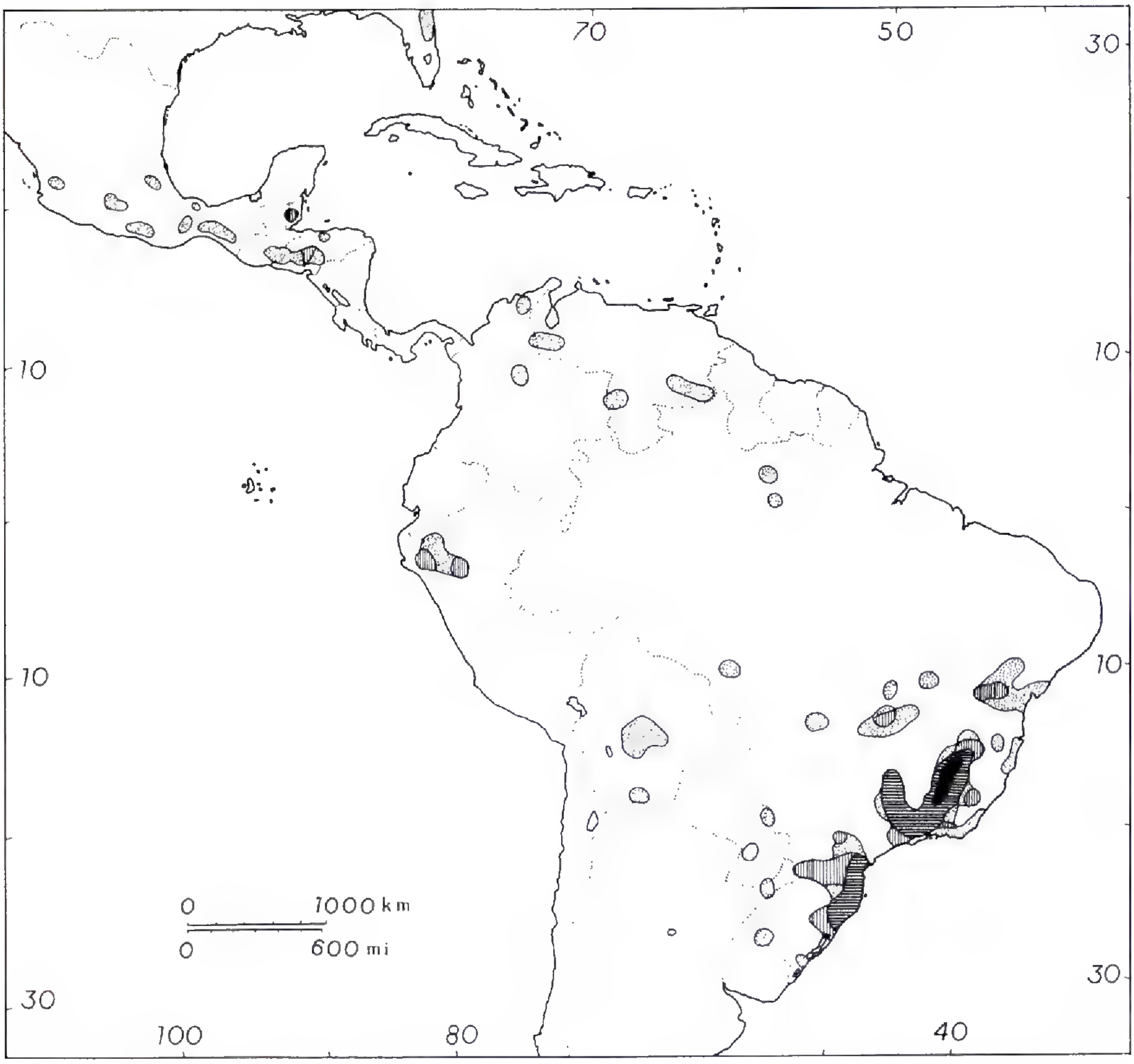
All three species comprising the *Agarista albiflora* group occur in the northern Andes. These species are likely rather primitive, and although it is clear from morphological and geographic evidence that the small-leaved *A. bracamorensis* and *A. subcordata* were probably derived from ancestors similar to the variable and widespread *A. albiflora,* these three species are only weakly linked in at least sometimes having cordate leaves (I).

Finally, the two species comprising the *Agarista revoluta* group (VIII) are characterized by their lack of gland-headed hairs (B; except rarely present on the ovary of *A. duckei*!) and their leaves with the blade often quite variable in extent of abaxial curvature (L^c). The capsules are often ovoid, with the valve margins sometimes slightly differentiated; the placentae are subapical, and the seeds are the longest (2–3.5 mm) of the section. The primitive species, *A. duckei,* occurs chiefly in the Guayana region, while the slightly more specialized *A. revoluta* grows in coastal "restingas" from the state of Bahia south to Estado do Rio in eastern Brazil.

There are insufficient data to determine the evolutionary interrelationships of these eight cladistic groups; all share the derived character-state of *Calluna*-type pith (E). In contrast, the African species, *Agarista salicifolia,* has slightly to strongly heterogeneous pith (Stevens, 1970). The species of *Agarista* sect. AGARISTA are obviously all closely related, although the extensive parallel evolution of characters and the frequency of character-state reversals obscure both intra- and intergroup relationships. Many examples of parallel evolution can be found among the various phylogenetic groups discussed above; these can be determined from FIGURE 1 and TABLE 4. Of the 27 characters used, at least 19 show some degree of intergroup parallelism (and also often intragroup parallelism or reversals), while 2 (O, T) of the remaining 8 show intragroup reversals and 1 (E) is invariant. In groups showing a large amount of homoplasy, such as *Agarista* sect. AGARISTA, the elucidation of cladistic relationships becomes extremely difficult. Thus, the conclusions reached here should be interpreted as very preliminary hypotheses, to be tested by the evaluation of additional characters (including anatomy and chemistry).

DISTRIBUTION AND ECOLOGY

As discussed above, the 30 species of *Agarista* recognized here are divided into two sections. Section AGAURIA, including the single species *A. salicifolia,* occurs in central Africa, Madagascar, Réunion, and Mauritius (Sleumer, 1938), while section AGARISTA, containing the remaining 29 species, occurs mainly in South America (MAP 1). Both sections are composed of basically montane



MAP 1. General distribution of *Agarista* sect. AGARISTA, showing center of diversity in southeastern Brazil. Pattern indicates number of taxa present: stipples, 1; vertical lines, 2; horizontal lines, 3 to 8; solid black, region of greatest diversity.

plants, with *A. salicifolia* occurring between 700 and 3500 m alt. and the many South American species growing from ca. 500 to 2700 m alt. However, *A. duckei,* a species of the Guayana Highland, can be found as low as 100 m, and *A. revoluta,* a taxon of coastal "restingas" in Brazil, frequently occurs near sea level. (*Agarista nummularia* and *A. pulchella* have also occasionally been collected at very low elevations near the coast.) Possible origins of this interesting montane tropical transatlantic distribution pattern shown by *Agarista* are discussed by Stevens (1970).

Section AGAURIA occurs in several widely scattered montane areas of central Africa but reaches its greatest morphological diversity in Madagascar (Sleumer, 1938). Species of section AGARISTA occur in five major geographic areas (see TABLE 5): the Coastal Plain of the southeastern United States (1 sp.—*Agarista populifolia*); the Mexican region—mountainous areas from central Mexico south to Honduras (2 spp.—*A. mexicana* and *A. sleumeri*); the Guayana Highland (1 sp.—*A. duckei*); the Andean region—mountainous areas from Bolivia to

TABLE 5. **Distribution of taxa of Agarista among the nations* of North, Central, and South America.**

1. UNITED STATES (1)
   A. populifolia†
2. MEXICO (3)
   A. mexicana var. *mexicana*
   A. mexicana var. *pinetorum*
   A. sleumeri†
3. GUATEMALA (1)
   A. mexicana var. *mexicana*
4. BELIZE (2)
   A. mexicana var. *mexicana*
   A. mexicana var. *pinetorum*
5. EL SALVADOR (1)
   A. mexicana var. *pinetorum*
6. HONDURAS (2)
   A. mexicana var. *mexicana*
   A. mexicana var. *pinetorum*
7. COLOMBIA (1)
   A. albiflora
8. ECUADOR (1)
   A. albiflora
9. PERU (3)
   A. albiflora
   A. bracamorensis†
   A. subcordata†
10. VENEZUELA (2)
    A. albiflora
    A. duckei
11. BOLIVIA (1)
    A. boliviensis†
12. BRAZIL (25)
    a. Pará (1)
       A. duckei
    b. Bahia (5)
       A. chapadensis
       A. coriifolia var. *coriifolia*
       A. oleifolia var. *glabra*
       A. revoluta var. *revoluta*
       A. revoluta var. *velutina*†
    c. Goiás (2)
       A. chapadensis
       A. oleifolia var. *glabra*
    d. Dist. Federal (2)
       A. chlorantha
       A. oleifolia var. *glabra*
    e. Mato Grosso (2)
       A. duckei
       A. oleifolia var. *glabra*
    f. Minas Gerais (16)
       A. angustissima†
       A. chlorantha
       A. coriifolia var. *coriifolia*
       A. coriifolia var. *bradei*†
       A. duartei†
       A. ericoides†
       A. eucalyptoides
       A. glaberrima†
       A. hispidula
       A. oleifolia var. *glabra*
       A. oleifolia var. *oleifolia*
       A. pulchella var. *cordifolia*
       A. pulchra†
       A. revoluta var. *revoluta*
       A. subrotunda†
       A. virgata†
    g. Estado do Rio/Guanabara (7)
       A. coriifolia var. *coriifolia*
       A. eucalyptoides
       A. hispidula
       A. oleifolia var. *oleifolia*
       A. organensis†
       A. revoluta var. *revoluta*
       A. uleana†
    h. SÃO PAULO (6)
       A. chlorantha
       A. eucalyptoides
       A. hispidula
       A. oleifolia var. *oleifolia*
       A. pulchella var. *cordifolia*
       A. pulchella var. *pulchella*
    i. Paraná (4)
       A. chlorantha
       A. niederleinii var. *acutifolia*
       A. niederleinii var. *niederleinii*
       A. pulchella var. *pulchella*
    j. Santa Catarina (7)
       A. chlorantha
       A. eucalyptoides
       A. minensis
       A. niederleinii var. *acutifolia*
       A. niederleinii var. *niederleinii*
       A. nummularia
       A. pulchella var. *pulchella*
    k. Rio Grande do Sul (5)
       A. eucalyptoides
       A. minensis
       A. niederleinii var. *acutifolia*
       A. niederleinii var. *niederleinii*
       A. nummularia
13. URUGUAY (1)
    A. eucalyptoides
14. PARAGUAY (1)
    A. paraguayensis
15. ARGENTINA (1)
    A. paraguayensis

*Within Brazil, states.

†Taxon endemic to nation or state.

Colombia (4 spp.—*A. albiflora, A. subcordata, A. bracamorensis, A. boliviensis*); and the Brazilian region—mountainous areas of southeastern Brazil (and adjacent Uruguay and Argentina) (22 spp.). With the exception of *A. duckei,* which has many populations in the Guayana Highland and a disjunct locality in western Mato Grosso, all species are endemic to one of these five regions.

The extremely diverse Brazilian region can be divided into northern and southern subunits, with the northern including the mountains of Minas Gerais and the adjacent states of São Paulo (northern part), Rio de Janeiro, Guanabara, Bahia, Goiás, and Mato Grosso, and the southern mountainous regions of the states of São Paulo (southern part) and Paraná south to Rio Grande do Sul and adjacent areas of Uruguay, northeastern Argentina, and Paraguay.

The northern subunit of the Brazilian region has the most species, with eighteen that are indigenous (see MAP 1). Within this area, the state of Minas Gerais has by far the most species, with fourteen (sixteen taxa), of which seven (eight taxa) are endemic; Estado do Rio/Guanabara is next with seven indigenous species (two endemics), followed by São Paulo (northern) with five species (no endemics) and Bahia with four species (one endemic variety). The southern subunit contains only seven indigenous species (eight taxa), of which four species (six taxa) are endemic. Only three species, *Agarista pulchella, A. chlorantha,* and *A. eucalyptoides,* occur in both subunits. TABLE 5 lists the species and varieties of *Agarista* occurring in or endemic to the various countries (and within Brazil, states) of North and South America.

The mountainous region of southeastern Brazil is a major center of diversity for many groups of vascular plants (see L. B. Smith, 1962; Good, 1964; Tryon, 1972). *Agarista* appears to have undergone extensive speciation (probably eco-geographic) in these mountains, since this region supports several groups of very derived taxa such as *A. coriifolia, A. glaberrima, A. angustissima, A. virgata, A. hispidula,* and *A. ericoides.* This concentration of *Agarista* species may be a relatively recent development, formed in response to Tertiary climatic and geologic changes (see Stevens, 1970).

The area of origin of the group is unknown. It is of interest that the primitive species *Agarista duckei* occurs in the floristically diverse Guayana Highland, while two other rather primitive taxa (*A. albiflora* and *A. subcordata*) occur in the geologically recent Andean region.

Agarista populifolia, of the southeastern United States, has its closest affinities with the montane Mexican taxa *A. sleumeri* and *A. mexicana.* There are many similarities between the deciduous forest formations of the eastern United States and the montane temperate forests of Mexico, and a number of species pairs have representatives in the two regions (see Miranda & Sharp, 1950; Dressler, 1954; Martin & Harrell, 1957; Graham, 1964, 1973; Rzedowski, 1965; and Gómez-Pompa, 1973). A similar disjunction pattern is seen in the related genus *Lyonia,* with *L. ferruginea* (Walter) Nutt. and *L. fruticosa* (Michaux) G. Torrey occurring in the southeastern U. S. and *L. squamulosa* Martens & Galeotti in the Sierra Madre Oriental of Mexico (Judd, 1981).

Although a few species such as *Agarista oleifolia, A. albiflora, A. mexicana,* and *A. eucalyptoides* have quite wide distributions, most (e.g., *A. pulchra, A. virgata, A. organensis, A. ericoides, A. angustissima, A. duartei, A. bracamo-*

rensis) are narrowly endemic. Most varieties and closely related species are more or less geographically isolated, but a few taxa, such as the varieties of *A. niederleinii,* seem to be chiefly elevationally/ecologically isolated.

The genus grows in a wide variety of habitats, but most species prefer acid soils and are sun-loving plants of open communities. Most also sprout readily from the base after fire or disturbance. Characteristic habitats include cerrado, rocky or grassy campo, boggy or marshy campo, shrub bogs, gallery forests along rivers or streams, thickets, open scrub, forest or thicket margins, elfin woodland or moist montane forests, rocky crests or slopes, coastal scrub/"restinga," sand dunes, savannas, and pine-oak forests. For detailed discussion of cerrado vegetation (along with lists of characteristic species), see Eiten (1972). Species may occur in iron-rich lateritic soils, sandstone regions, white sands, or highly organic soils.

TAXONOMIC CRITERIA

Because of the extensive parallel evolution and character-state reversals within *Agarista,* different species can be separated only by using sets of vegetative and reproductive characters. Morphological entities that have no major internal discontinuities and that are separated from other, similar entities by consistent morphological gaps are considered to be species. They have definite geographic distributions and ecological preferences. Many species, such as *A. pulchra, A. virgata, A. organensis, A. ericoides, A. angustissima, A. duartei,* and *A. bracamorensis,* are narrowly endemic. Most species (and varieties) are probably isolated by differences in distribution, ecology, and/or genetic composition. The term "variety" has been used for the morphologically distinctive geographic (or ecological) subunits comprising widespread and/or variable species (see Judd, 1981). Varieties have only very slight morphological gaps between them, may intergrade, and often differ in only one (or very few) aspect(s) of indumentum or leaf morphology.

The taxonomic usefulness of (and the variation within) the various characters used in this revision are discussed below. Characters most useful in species delimitation include: 1) leaf vernation, size, shape, apex and base types, petiole length, and extent to which the margin is revolute; 2) inflorescence length; 3) unicellular indumentum of the abaxial leaf surface and of the inflorescence axes and other reproductive structures (especially calyx, corolla, and ovary); 4) calyx length and, to a lesser extent, corolla color and length; 5) placenta position (in fruit); and 6) seed length.

HABIT

The species of *Agarista* vary from small, sparsely and erectly branched subshrubs such as *A. ericoides, A. virgata, A. hispidula, A. duartei,* and *A. nummularia* to moderate-sized, laxly branched trees up to 6–8(–20) m tall such as *A. populifolia, A. sleumeri,* and *A. mexicana.* The branching pattern, including internode length, density of branching, and orientation of branchlets, is quite variable but is sometimes useful in distinguishing between species (e.g., *A.*

virgata and *A. pulchra*; see key). Although the bark is always longitudinally furrowed, it is very poorly developed in the smaller species (e.g., *A. virgata, A. duartei, A. ericoides*). It is occasionally of taxonomic interest, such as in separating *A. populifolia,* in which the bark is thin and shallowly furrowed, from the related *A. mexicana* and *A. sleumeri,* in which it is thick, corky, and deeply furrowed. Cerrado species such as *A. eucalyptoides* tend to have contorted trunks and thick, corky bark, characters very common in this vegetation type (see Eiten, 1972). Most species sprout readily from the base after fire or disturbance.

As in most other members of the Andromedeae, the shoot meristem in *Agarista* has a limited life span, and growth in height is achieved by a succession of equivalent axillary, orthotropic shoots (Lems, 1962). All species show Leeuwenberg's Model of growth (see Hallé, Oldeman, & Tomlinson, 1978, for description) or a slight variation of this architectural pattern. Floral buds are usually produced in the leaf axils of the distal portion of the shoot, although they may be restricted to those at or very near the apex. The shoot apex typically aborts, but in some species (e.g., *A. angustissima, A. coriifolia, A. glaberrima*) it is converted into a terminal inflorescence (with the leaves gradually grading into bracts). The inflorescences overwinter within the buds, with meiosis presumably occurring in the spring (see Lems, 1962).

Twigs

The branchlets vary from terete to slightly angled. Pith is of the *Calluna*-type in all American species and varies from non- to clearly chambered. Its structure is frequently of taxonomic value (see key) and is especially useful in separating *Agarista paraguayensis, A. populifolia,* and *A. sleumeri* from *A. mexicana.*

Indumentum

The indumentum of *Agarista* is of three distinct types: unicellular hairs; multicellular, multiseriate-stalked, gland-headed hairs; and papillae. Although the presence or absence of multicellular, gland-headed hairs has been much used in the taxonomy of the genus (Sleumer, 1959), this character is actually too variable to be of much taxonomic significance. Of the 29 species comprising *Agarista* sect. Agarista, 13 have both glandular-pubescent and nonglandular forms. Only *A. virgata* is consistently glandular-pubescent. However, this taxon has been very poorly collected and nonglandular forms may eventually be discovered. Fifteen species consistently lack glandular hairs. Glandular-pubescent and nonglandular individuals frequently occur intermixed in the same population (e.g., *Judd 2609, A. populifolia*). There is also much variation in density and distribution of multicellular gland-headed hairs. At one extreme are plants with glandular hairs on the young twigs, midvein (or even lamina) of both leaf surfaces, inflorescence axes, pedicels, and calyx lobes; other individuals may have such hairs only on the inflorescence axes, or only along the leaf margins (i.e., leaves ± glandular-ciliate). In a few species such as *A. angustissima* and *A. duartei,* glandular hairs are only present on juvenile plants.

Finally, *A. duckei* is unique because of its occasionally glandular-pubescent capsules. However, because of the extensive intrapopulational (and developmental) variation in glandular indumentum, it has not been possible to use this character at either the specific or the infraspecific level. The several groups of extremely similar taxa (e.g., *A. nummularia* var. *nummularia* and *Leucothoë* (*Agarista*) *nummularia* var. *floccigera*; *A. chlorantha* and *A. serrulata*; *A. hispidula* and *A. intermedia*; *A. ericoides, Leucothoë* (*Agarista*) *lycopodioides,* and *L.* (*Agarista*) *acicularis*; *A. subrotunda* and *A. pistrix*; and *A. oleifolia* var. *oleifolia* and *Leucothoë* (*Agarista*) *oleifolia* var. *hispidula*) that were recognized by Sleumer (1959) and that differ chiefly in the presence or absence of such hairs have been considered conspecific.

All species of *Agarista* have at least a few unicellular hairs, and the distribution and density of such hairs is frequently of taxonomic significance (see keys). Several taxa—*A. mexicana* var. *pinetorum, A. revoluta* var. *velutina, A. subrotunda, A. chapadensis,* and *A. paraguayensis*—have a distinctive dense covering of unicellular hairs on their abaxial leaf surfaces. The unicellular indumentum of the inflorescence axis and other reproductive structures (especially calyx, corolla, and ovary) was found often to be of systematic value. Thus, the inflorescence indumentum is useful in distinguishing *A. glaberrima* from *A. boliviensis* and *A. eucalyptoides, A. virgata* from *A. nummularia, A. oleifolia* var. *oleifolia* from var. *glabra,* and *A. pulchra* from *A. pulchella.* Several taxa (e.g., *A. paraguayensis, A. revoluta* var. *velutina,* and *A. hispidula*) are easily distinguished from related ones due to their abaxially pubescent corollas, and the indumentum of the ovary and calyx is very useful in separating *A. mexicana, A. sleumeri,* and *A. populifolia.* However, such characters must be used with care since many species are quite variable in indumentum. Although the unicellular indumentum of the twigs is usually too variable to be of much taxonomic use, it is distinctive in a few species. For example, the hairs are ferrugineous in *A. eucalyptoides* and elongate in *A. albiflora.*

Abaxially papillose leaves are found only in the African species, *Agarista salicifolia* (sect. AGAURIA); all the American species (sect. AGARISTA) lack such papillae.

LEAVES

Characters of leaf vernation, size, shape, apex and base types, thickness, petiole length, and extent to which the margin is revolute are extremely important in the taxonomy of *Agarista* sect. AGARISTA. Most species of *Agarista* have leaves that are revolute in bud; consequently the mature leaves often have a faint longitudinal "fold" line on each side of the midvein. However, *A. duartei, A. angustissima,* and sometimes *A. glaberrima* have strongly adaxially folded leaves. The mature leaves may be more or less flat with a plane to only very slightly revolute margin (many species), strongly to slightly adaxially folded (*A. duartei, A. angustissima, A. glaberrima*), or clearly abaxially curved with more or less strongly revolute margins (e.g., *A. organensis, A. hispidula, A. chlorantha, A. ericoides*). There is great variation in size and shape of the lamina—from 0.4–1.2 cm long in *A. ericoides* to 4–13 cm long in *A. sleumeri,*

and from linear in *A. angustissima* to often nearly orbicular in *A. nummularia.* Numerous examples of the taxonomic usefulness of leaf shape and size are evident in the key. The petiole ranges from very short (ca. 1.5 mm in *A. ericoides*) to very long (to ca. 40 mm). The often long, slender, flexuous petioles of *A. eucalyptoides, A. glaberrima,* and *A. boliviensis* are especially distinctive. The apex and base of the lamina, although often showing much infraspecific variation, are sometimes useful at the species level. Many species have leaves that vary from acute to rounded with a small mucro at the apex, and from slightly cordate to rounded or cuneate at the base. The leaf apex is useful in distinguishing *A. duckei, A. revoluta,* and *A. albiflora*; the base, in separating *A. minensis* from *A. pulchella* (see key). *Agarista populifolia, A. mexicana,* and *A. sleumeri* are distinctive due to their consistently ovate leaves with acuminate apices. Finally, although most species have moderately coriaceous leaves, *A. coriifolia* and its relatives have thickly coriaceous blades that are rather inflexible when dry.

The leaves of most species are entire but those of *Agarista boliviensis* are distinctive in having crisped/undulate margins, and those of *A. populifolia* are often serrate. In this species each tooth is associated with a multicellular gland-headed hair. The margins of several Brazilian species are sometimes glandular-ciliate due to the presence of multicellular gland-headed hairs.

Many species have glandular "patches" or "dots" along the midvein on the abaxial epidermis. These glandular regions (which should not be confused with the much smaller gland-headed hairs found in some species) seem to be associated with the secondary veins and are variable in size and shape. They are sometimes of taxonomic interest, as in distinguishing the varieties of *Agarista coriifolia.*

All species have reticulodromous venation, with a rather dense vein reticulum and all orders more or less equally prominent (Lems, 1964; Judd, 1979).

Inflorescence

The flowers of *Agarista* are borne in axillary (or, less commonly, terminal) racemes or panicles on branches of the previous season, although in *A. organensis* the inflorescences are often reduced to solitary axillary flowers or few-flowered clusters, and in several species (e.g., *A. minensis*) the axis is so shortened that the inflorescence is nearly a fascicle. There is always a single inflorescence per leaf axil. Terminal flowers are usually lacking, with the apex of the raceme simply aborting, so the inflorescences are polytelic (Weberling, 1965). However, in *A. populifolia* a few of the flowers composing the raceme are rarely replaced by two-flowered clusters—i.e., one of the bracteoles of the pedicel subtends a secondary flower. This also occurs in *A. pulchella* and *A. coriifolia* var. *bradei,* resulting in a small panicle in which the two- to many-flowered inflorescence branches have terminal flowers, although the apex of the primary axis aborts. However, the apices of even the secondary axes (branches) of many panicles abort (see panicles of *A. coriifolia, A. virgata, A. glaberrima*). The few-flowered axillary fascicles (or short racemes) of *A. organensis* also at least sometimes have terminal flowers, and it is probable that

the pedicel of the "solitary axillary flower" with its several bracteoles actually represents a very reduced inflorescence axis (i.e., a terminal-flowered raceme). Thus, monotelic (or partly monotelic) inflorescences occur in a few species of the genus. This inflorescence type is, according to Weberling (1965), more primitive than the polytelic type, and the presence of more or less monotelic inflorescences in this group (along with their variation in position) may indicate its low level of advancement. In reproductive characters most species of *Agarista* are certainly less specialized than those of *Lyonia, Craibiodendron,* or *Pieris* (Judd, 1979).

There is great interspecific variation in inflorescence length—from at most ca. 1.5 cm in *Agarista organensis* or *A. minensis* to over 20 cm in *A. coriifolia.* This character is thus taxonomically useful and has been employed in separating *A. minensis* from *A. pulchella, A. angustissima* from *A. duartei,* and *A. organensis* from *A. chlorantha,* among others.

FLOWERS

All species have actinomorphic, perfect, pendulous flowers, although the pedicel curves upward as the fruits begin to develop, ultimately placing the capsules in an erect position. The flowers of all species are five-merous and quite fragrant. Those of *Agarista populifolia* are visited chiefly by bumblebees (*Bombus*); no information is available on the pollination of the many South American species.

The pedicel varies in length from only 1.5–3 mm in *Agarista bracamorensis* to 14–15 mm in *A. angustissima, A. coriifolia,* and *A. pulchella.* This is not a very useful taxonomic character since the pedicel tends to elongate as the flowers and fruits develop. All species have a clearly developed articulation between the pedicel and the receptacle, its position varying from at to ca. 3 mm below the insertion of the calyx. In all species the pedicel is subtended by a single bract, the size of which is usually too uniform to be of taxonomic importance. Each pedicel in *Agarista* usually has a pair of bracteoles, although there are occasionally three to many in a few taxa. The bracteoles are usually positioned along the pedicel from the base to near the midpoint; they may rarely even be found near its apex. The bracteoles are characteristically minute (see descriptions) and linear to triangular or ovate-triangular; very rarely they subtend secondary flowers. The number, size, and shape of the bracteoles are too uniform to be useful at the species level.

The calyx is composed of five persistent, more or less triangular, imbricate sepals that are connate only at the very base. Stomata are present only on the abaxial surface (Stevens, 1971). The lobes show some interspecific variation in length (e.g., 0.5–1.5 mm in *Agarista bracamorensis,* 3–6 mm in *A. ericoides*). This character is thus frequently of taxonomic significance, and it has been used to distinguish *A. chlorantha* from *A. organensis* and *A. nummularia* from *A. pulchella.* The apex varies from acuminate to acute and is usually too uniform to be of systematic importance. However, *A. chlorantha* typically has acute tips, while those of the related *A. hispidula* are usually acuminate.

The corolla is always sympetalous and deciduous. Stomata are present on

the outer surface but lacking on the inner (Stevens, 1971). In most species the corolla is more or less cylindrical, but in a few such as *Agarista albiflora, A. duckei,* and *A. hispidula* it may be urceolate or nearly so. The corolla is most often white (or greenish white) or white with a pinkish to reddish tinge toward the mouth, but in some species (e.g., *A. revoluta, A. coriifolia* var. *bradei, A. oleifolia* var. *glabra, A. ericoides*) it is frequently red. Its length varies from 5–8 mm in *A. niederleinii* var. *acutifolia* to 10.5–16 mm in *A. oleifolia* var. *glabra.* The shape, size, and color of the corolla are only slightly taxonomically useful in *Agarista,* due both to the overall uniformity of these characters within the genus and to their considerable variation in some taxa.

The flowers of all species of *Agarista* have ten stamens. These are arranged in two whorls and inserted at the base of the corolla; the outer whorl is opposite the corolla lobes. The stamens are always included and are arranged in a tight ring, with the anther pores facing inward. The filaments are slender, flattened, geniculate, nonappendaged, and slightly swollen near the base. They are covered with long unicellular hairs, especially near the base. Filament length varies from 3–4.5 mm in *A. eucalyptoides* and ca. 3.5 mm in *A. subcordata* to 6.5–8.5 mm in *A. oleifolia* var. *glabra.* A white line or triangular patch of disintegration tissue is present on the back of each anther lobe near the apex, but this tissue is only poorly developed in several species. Because of the consistency of the androecial characters within *Agarista,* they have seldom been used at the species level.

The ovary is superior. The placentae are axile and are borne subapically to basally on a central columella. Species with more or less central (e.g., *Agarista oleifolia, A. pulchella, A. paraguayensis*) or basal (e.g., *A. salicifolia*) placentae have very deeply impressed styles. Placenta position is an important taxonomic character and frequently links related groups of species—for example, sect. AGARISTA (subapical to central) vs. sect. AGAURIA (basal), and the *A. oleifolia* species group (± central) vs. the *A. coriifolia* group (± subapical). The ovary shape varies from ovoid to subglobose, but this variation (like that in placenta position) is better expressed in the mature fruit.

FRUITS AND SEEDS

The fruits of *Agarista* are five-valved, subglobose or short-ovoid to ovoid, loculicidal capsules with pale, unthickened (or occasionally very slightly thickened near apex) sutures. Within *Agarista* sect. AGARISTA, the capsules tend to be rather uniform in size and shape, but those of *A. niederleinii* and *A. uleana* are distinctive due to their large size and their thick walls. Placenta position is best observed in mature fruits and, as mentioned above, is a very valuable taxonomic character within the genus. The variation in placental position within *Agarista* sect. AGARISTA is shown in TABLE 4 and in the key.

The seeds are very small, brown, and scobiform, and they have a thin testa composed of very elongate cells. Species with central placentae tend to have short (0.5–1.4(–1.6) mm) seeds, while those with subapical placentae usually have longer (1–3(–3.5) mm) ones. The seeds of *Agarista salicifolia* are 3–4 mm long (Sleumer, 1938).

VEGETATIVE ANATOMY

The vegetative anatomy of the genus has not been studied in detail. However, pith type was found to be an important taxonomic character: it is *Calluna*-type in all American species (see Stevens, 1970) and slightly to very heterogeneous in the African species, *Agarista salicifolia* (Stevens, 1970). In addition, it remains more or less solid in many American species but becomes nearly hollow in *A. paraguayensis,* or irregularly to regularly chambered/diaphragmed in several taxa (see descriptions). The pith is always chambered in *A. populifolia, A. sleumeri,* and *A. minensis.* Stevens (1970) has pointed out that *A. salicifolia* has epidermal cells that are usually not tall and are rarely divided periclinally, and a single-layered hypodermis that is more or less continuous in its leaves. In contrast, the American species of *Agarista* have epidermal cells that are usually tall and with periclinal dividing walls, and a hypodermis of at most one or two cells (in cross section) near the larger veins. The vascular bundles of the midrib and petiole are unifacial, with very prominent bundle-associated fibers (Niedenzu, 1889; Stevens, 1970). The xylem anatomy has been studied by Cox (1948), who placed *A. salicifolia* in his tribe Cassiopeae and retained the species of *Agarista* sect. AGARISTA within the Andromedeae.

TAXONOMIC TREATMENT

Agarista D. Don ex G. Don, Gen. Syst. **3:** 837. 1834. *Leucothoë* D. Don sect. *Agastia* DC. Prodr. **7:** 603. 1839. *Leucothoë* D. Don subg. *Agarista* (D. Don ex G. Don) Drude *in* Engler & Prantl, Nat. Pflanzenfam. IV. **1:** 42. 1889. LECTOTYPE SPECIES: *Agarista nummularia* (Cham. & Schldl.) G. Don.

Leucothoë D. Don sect. *Agauria* DC. Prodr. **7:** 602. 1839. *Agauria* (DC.) J. D. Hooker *in* Bentham & Hooker, Gen. Pl. **2:** 586. 1876. LECTOTYPE SPECIES: *Agauria salicifolia* (Comm. ex Lam.) J. D. Hooker (= *Agarista salicifolia* (Comm. ex Lam.) G. Don).

Amechania DC. Prodr. **7:** 578. 1839. LECTOTYPE SPECIES: *Amechania subcanescens* DC. (= *Agarista chlorantha* (Cham.) G. Don).

Evergreen shrubs or trees with longitudinally furrowed bark and terete to slightly angled branches; pith *Calluna*-type [or slightly to very heterogeneous],[3] nonchambered to clearly chambered. Indumentum of unicellular hairs and often multicellular, multiseriate, long-stalked, gland-headed hairs. Buds conical or slightly flattened and triangular in outline, with 2 to 4 (to 6) imbricate scales. Leaves alternate (to subopposite or nearly 3-whorled at some nodes), simple, petiolate, revolute (or convolute) in bud, often reddish on young shoots, coriaceous, frequently with gland-headed hairs on midvein or along margin (rarely also on lamina), often with unicellular hairs on midvein (and densely covering abaxial surface) [sometimes papillose abaxially]; margin entire (or undulate, to obscurely to clearly serrate, or serrulate/ciliate due to presence of gland-headed hairs); venation reticulodromous, the vein reticulum rather dense and with all

[3]Characters given within brackets apply only to the African species, *A. salicifolia.*

orders more or less equally prominent; petiole vascular bundle unifacial. Inflorescences overwintering within bud with meiosis occurring after emergence, axillary (or terminal) racemes or panicles; flowers perfect, 5-merous, usually fragrant, in axil of small (to rarely large and foliaceous) bract, with 2 (rarely several), bracteoles at or near base to near midpoint of pedicel. Calyx of 5 imbricate lobes, articulate with pedicel, persistent in fruit; corolla cylindrical to urceolate, with 5 short, imbricate lobes, (greenish) white to red, glabrous to densely covered with unicellular hairs abaxially, glabrous adaxially; stamens 10, in 2 whorls, inserted at base of corolla, the filaments flattened, geniculate, with long unicellular hairs, somewhat expanded near base, lacking spurlike appendages, the anthers more or less ovoid, minutely papillose to nearly smooth, lacking apical awns, dehiscing by large, introrse-terminal, elliptic pores, with white line or triangular patch of disintegration tissue on back of each lobe near apex, the pollen tricolporate, in tetrahedral tetrads, without viscin strands; stigma truncate to capitate, obscurely 5-lobed, minutely papillose, the style columnar, slightly swollen [not swollen] near apex, straight, with 5-fluted central canal, slightly to strongly impressed into apex of ovary and usually slightly exserted, the ovary superior, 5-locular, glabrous to densely covered with unicellular hairs (very rarely with few gland-headed hairs), with the placentae axile, subapical to central [basal] on persistent columella, slightly bilobed, bearing numerous anatropous ovules; nectariferous disc an enlargement of base of ovary wall, variously developed and lobed. Capsules loculicidal, subglobose, short-ovoid to ovoid, sutures unthickened (or very slightly thickened near apex), but not separating from valves at dehiscence (margins of valves whitish), placentae persistent on columella. Seeds very small, brown, scobiform, the testa thin, composed of single layer of very much elongated, thin-walled cells; embryo small, straight, more or less allantoid, white, with 2 small cotyledons, central in cross section, surrounded by fleshy endosperm. Germination epigeal(?). $2n = 24$ (*Agarista populifolia*).

The name *Agarista* is taken from Greek mythology—the beautiful daughter of Clisthenes—in reference to the beauty of the flowers (see G. Don, 1834).

DISTRIBUTION. South America—southeastern Brazil (from Bahia and Goiás south to Rio Grande do Sul), Uruguay, northeastern Argentina, and Paraguay, along Andes from Bolivia and northern Peru to Colombia, mountains of southern Venezuela and adjacent Brazil (Pará); Central and North America—mountains of El Salvador and Honduras north to Mexico (Hidalgo, México, Jalisco), and on United States Atlantic Coastal Plain (from Florida to South Carolina); MAP 1. Also in central Africa, Madagascar, Réunion, and Mauritius (Sleumer, 1938, *fig. 1*).

NUMBER OF SPECIES (TAXA): 30 (55).

MEASUREMENTS AND TERMINOLOGY

All measurements (except plant height, which was taken from information included on specimen labels or recorded in the field) included in the descriptions of species have been taken directly from dried herbarium material. The width

of the calyx lobes was measured midway between the apex and the point where they join the adjacent lobes; the width of all other structures was measured at the widest point. The values for inflorescence length refer to the range of variation in the longest inflorescence per specimen (and were determined by surveying total available herbarium material).

As used here, "glabrous" and "pubescent" refer to the presence or absence of unicellular hairs; the presence, distribution, and density of multicellular, gland-headed hairs are described separately.

SPECIMENS EXAMINED

In the citation of specimens, abbreviations of institutions follow the seventh edition of *Index Herbariorum* (Holmgren, Keuken, & Schofield, 1981). In order to conserve space, only selected specimens have been cited. The locations of types cited but not seen have been taken from Sleumer (1959).

KEY TO THE SECTIONS AND SPECIES OF AGARISTA

1. Leaves with abaxial epidermis papillose; capsules with placentae basal; [Africa]; (sect. AGAURIA). . . . . [30.] *A. salicifolia* (for key to infraspecific taxa, see Sleumer, 1938).
1. Leaves with abaxial epidermis nonpapillose; capsules with placentae subapical to central; [Americas]; (sect. AGARISTA).
   2. Leaves moderately to strongly adaxially folded.
      3. Leaves 0.6–2.5(–3) cm wide, narrowly to widely ovate, petiole 10–32 mm long. . . . . 27. *A. glaberrima.*
      3. Leaves 0.1–0.5 cm wide, ± linear, petiole 2–13 mm long.
         4. Stems glabrous; inflorescences axillary or terminal racemes or panicles to 3–6 cm long, axis glabrous; leaves (1.7–)3–7 cm long. . . . . 28. *A. angustissima.*
         4. Stems glabrous to densely pubescent; inflorescences axillary racemes to 0.3–1.5 cm long, axis very slightly to densely pubescent; leaves 1.2–3.5(–4) cm long. . . . . 29. *A. duartei.*
   2. Leaves plane to strongly revolute, always revolute in bud.
      5. Petiole slender, flexuous, elongate, 6–40 mm long.
         6. Inflorescence axis glabrous; capsules 4–8 by 6–8 mm; leaves often slightly adaxially folded. . . . . 27. *A. glaberrima.*
         6. Inflorescence axis moderately to densely pubescent; capsules 3–5 by 4–6.5 mm; leaves ± flat.
            7. Leaves ovate; inflorescence axis with whitish hairs. . . . . 25. *A. boliviensis.*
            7. Leaves oblong to ovate; inflorescence axis with ferrugineous hairs. . . . . 26. *A. eucalyptoides.*
      5. Petiole stout and/or short, not flexuous, 0.5–15(–18) mm long.
         8. Leaves 0.4–2.5(–3.5) by 0.1–1.6(–2) cm.
            9. Leaf margin ± plane (to very slightly revolute, especially near base), lamina ± flat.
               10. Inflorescence axis glabrous.
                  11. Leaf blade with length/width quotient > 1.8; corolla 7.5–13 mm long; filaments 5–6.5 mm long. . . . 16. *A. pulchella.*
                  11. Leaf blade with length/width quotient < 1.8; corolla 6–8.5 mm long; filaments 3.5–5 mm long.
                     12. Multicellular, gland-headed hairs present on leaves and twigs; branches rigidly ascending and wandlike, with internodes usually to only ca. 0.5 cm long; leaves 0.4–1.3 cm wide. . . . . 18. *A. virgata.*
                     12. Multicellular, gland-headed hairs lacking; plants ± widely to erectly branched, with internodes usually to 0.5–2 cm long; leaves 0.8–2.2 cm wide. . . . . 10. *A. pulchra.*
               10. Inflorescence axis sparsely to densely pubescent.
                  13. Abaxial leaf surface ± densely pubescent. . . . . 11. *A. subrotunda.*
                  13. Abaxial leaf surface ± glabrous (but often with few unicellular hairs on midvein).
                     14. Sepals 2.5–5 mm long. . . . . 17. *A. nummularia.*
                     14. Sepals 0.8–2.7 mm long.

15. Capsules with placentae ± central.
    16. Inflorescence axis to 0.5–1.5(–2.5) cm long; leaf blade with length/width quotient usually > 3, cuneate to truncate at base. ..... 15. *A. minensis.*
    16. Inflorescence axis to 2–7(–12) cm long; leaf blade with length/width quotient usually < 3, cordate to rounded at base. ..... 16. *A. pulchella.*
15. Capsules with placentae ± subapical.
    17. Hairs of inflorescence axis to (0.15–)0.2–0.4 mm long, straight to curved. ..... 1. *A. albiflora.*
    17. Hairs of inflorescence axis to 0.05–0.15(–0.17) mm long, curved.
        18. Leaves cuneate to rounded at base; inflorescence axis usually 1.5–3.5 cm long. . . 23. *A. niederleinii.*
        18. Most leaves at least slightly cordate at base; inflorescence axis usually 2–28 cm long.
            19. Stems moderately to densely pubescent; inflorescence axis to (1.5–)2–5.5 cm long. ..... 16. *A. pulchella.*
            19. Stems glabrous to sparsely pubescent; inflorescence axis to 4–28 cm long.
                20. Petioles 1–2.5 mm long, lamina lacking prominent abaxial glands along midvein, margin usually at least slightly undulate and frequently very slightly revolute; [Peru]. ..... 2. *A. subcordata.*
                20. Petioles 1.5–6 mm long, lamina without above combination of characters, with or without conspicuous abaxial glands, margin usually plane; [SE Brazil].
                    21. Leaf blades with length/width quotient (1.5–)1.8–2.5, prominent abaxial glands present along midvein; inflorescence axis moderately to densely pubescent. . . . 9. *A. coriifolia.*
                    21. Leaf blades with length/width quotient 0.9–1.7, usually lacking prominent abaxial glands; inflorescence axis very sparsely to moderately pubescent. ..... 10. *A. pulchra.*
9. Leaf margin slightly to strongly revolute and/or lamina slightly to clearly abaxially curved.
    22. Corolla very sparsely to densely pubescent abaxially.
        23. Calyx lobes 2–5.5 mm long; corolla abaxially sparsely to densely pubescent; seeds ca. 0.6–1.5 mm long; erect shrub 1–2.5 m tall, of inland habitats. ..... 21. *A. hispidula.*
        23. Calyx lobes 0.9–1.6 mm long; corolla abaxially with very few unicellular hairs near apex (or glabrous); seeds ca. 2–3.5 mm long; shrub or gnarled tree to 3(–6) m tall, of coastal scrub. ..... 5. *A. revoluta.*
    22. Corolla glabrous abaxially.
        24. Capsules with placentae ± central; leaves 0.1–0.25 cm wide. ..... 22. *A. ericoides.*
        24. Capsules with placentae ± subapical; leaves 0.15–2.2 cm wide.
            25. Flowers solitary in leaf axils or borne on fasciclelike racemes to 1.5 cm long; plants lacking gland-headed hairs; calyx lobes 1–2 mm long; [Serra dos Orgãos]. ..... 20. *A. organensis.*

25. Flowers in axillary (rarely terminal) racemes to (1–)1.5–9.5 cm long; plants with or without gland-headed hairs; calyx lobes variable; [not of the Serra dos Orgãos].
    26. Calyx lobes 2.5–5.5 mm long; corolla 7–11.5 mm long; leaves clearly cordate at base; inflorescence axis and pedicels with or without gland-headed hairs. ..... 19. *A. chlorantha.*
    26. Calyx lobes 0.5–2.7 mm long; corolla 4.5–9 mm long; leaves cuneate to rounded or slightly cordate at base; inflorescence axis and pedicels lacking gland-headed hairs.
        27. Leaves 0.4–2.2 cm wide, with margins revolute frequently to varying degrees even within single plant; valves of mature capsules frequently ± whitish bordered; capsules ovoid to globose or subglobose; [coastal "restingas"]. ..... 5. *A. revoluta.*
        27. Leaves 0.25–1.3 cm wide, with margins more uniformly revolute within single plant; valves of capsules not obviously bordered; capsules subglobose or short-ovoid; [mountainous habitats].
            28. Capsules robust, 4.5–6.5 by 6.5–8.5 mm; inflorescence axis to 1.5–3.5(–4.5) cm long; [SE Brazil]. .. .. 23. *A. niederleinii.*
            28. Capsules smaller, 4–5 by 4.5–6 mm; inflorescence axis to 5–10 cm long; [Peru].
                29. Leaves 0.25–0.7 by 0.8–1.5 cm, lamina ± strongly revolute, pedicel 1.5–3 mm long. .... 3. *A. bracamorensis.*
                29. Leaves 0.6–1.3 by 1.2–3.1 cm, lamina plane to slightly revolute, pedicel 3.5–7 mm long. .... 2. *A. subcordata.*

8. Leaves 1.5–11.2 by 0.3–4.5(–5) cm.
    30. Lamina clearly to strongly revolute, slightly to strongly abaxially curved.
        31. Inflorescence axis to 0.7–1.5 cm long; leaf apex short-acuminate to elongate-mucronate, mucro usually to 1.5–2 mm long; [Venezuela; Pará and Mato Grosso, Brazil]. ..... 4. *A. duckei.*
        31. Inflorescence axis to 1.5–10 cm long; leaf apex acute- to rounded-mucronate, mucro usually to only 1 mm long.
            32. Leaf apex obtuse- to retuse-mucronate; valves of mature capsules often ± white bordered; [coastal "restingas," E Brazil]. ..... 5. *A. revoluta.*
            32. Leaf apex acute- to obtuse-mucronate; valves of capsules ± unbordered; [mountainous habitats, northern Andes]. .. .. 1. *A. albiflora.*
    30. Lamina plane to only very slightly revolute, ± flat.
        33. Abaxial leaf surface ± densely covered with unicellular hairs, at least parts of surface completely obscured.
            34. Capsules with placentae ± central; seeds 0.9–1.8 mm long; pith ± solid to hollow, often with very sparse, thin septa; [Paraguay, Argentina]. ..... 13. *A. paraguayensis.*
            34. Capsules with placentae ± subapical; seeds 1.3–3 mm long; pith ± solid to irregularly chambered, the septa thick to thin, closely spaced.

35. Inflorescence axis to 0.5–2(–4) cm long; leaves ovate, apex acuminate; [Mexico and Central America]. ..... 6. *A. mexicana.*
35. Inflorescence axis to 4–7 cm long; leaves ovate to elliptic or oblong, apex acute- to retuse-mucronate; [E Brazil].
    36. Leaf base cordate; pedicels 5–12.5 mm long. ..... 11. *A. subrotunda.*
    36. Leaf base rounded to cuneate; pedicels 3–7 mm long. ..... 12. *A. chapadensis.*

33. Abaxial leaf surface lacking unicellular hairs to ± sparsely pubescent, surface not obscured.
    37. Capsules with placentae ± central; seeds 0.5–1.5 mm long.
        38. Corolla very sparsely to sparsely pubescent; pith ± solid to hollow or with very sparse, thin septa; [Paraguay, Argentina]. ..... 13. *A. paraguayensis.*
        38. Corolla glabrous; pith ± solid to irregularly or clearly chambered, the septa thin to thick, ± closely spaced; [SE Brazil].
            39. Inflorescence axis to 0.5–1.5 cm long; leaves 0.3–1(–1.7) cm wide, length/width quotient usually > 3, ± straight sided, base cuneate to truncate, apex rounded- to bluntly acute-mucronate (never narrowly acute), petiole 2–6 mm long. ..... 15. *A. minensis.*
            39. Inflorescence axis to 2–12 cm long; leaves various, but without above combination of characters.
                40. Leaves ± ovate, 1.2–4.5(–5) cm long, margin usually convex-curved when viewed from above, base ± cordate, petiole 1.5–5 mm long.
                    41. Lamina with abaxial glands lacking or very inconspicuous along midvein near base, thinly coriaceous and flexible when dry; [Paraná, Santa Catarina, São Paulo]. ..... 16. *A. pulchella.*
                    41. Lamina with prominent abaxial glands along midvein near base, thickly coriaceous and quite inflexible when dry; [Minas Gerais].
                        42. Inflorescence axis ± moderately pubescent. ..... 9. *A. coriifolia.*
                        42. Inflorescence axis glabrous. ..... 10. *A. pulchra.*
                40. Leaves ovate to elliptic or oblong, 2–12.5 cm long, margin often ± straight when viewed from above, base cuneate to slightly cordate, petiole 2–11.5 mm long. ..... 14. *A. oleifolia.*
    37. Capsules with placentae ± subapical; seeds 1–3.2 mm long.
        43. Inflorescence axis usually moderately to densely covered with ferrugineous unicellular hairs. ..... 26. *A. eucalyptoides.*
        43. Inflorescence axis glabrous to densely pubescent, hairs not ferrugineous.
            44. Inflorescence axis to 0.5–3 cm long.
                45. Leaves uniformly ovate, apex acuminate.
                    46. Leaf margin conspicuously crisped/undulate. ..... 25. *A. boliviensis.*
                    46. Leaf entire to serrate, margin not conspicuously crisped/undulate.

47. Capsules (3–)4–6 mm long, with thickened, ± warty/roughened walls; [SE Brazil]. ..... 24. *A. uleana.*
47. Capsules 3–4.5 mm long, with thin, ± smooth walls; [North and Central America].
    48. Ovary very sparsely to densely pubescent; pith nonseptate to septate; bark prominently and deeply furrowed, corky. ..... 6. *A. mexicana.*
    48. Ovary glabrous; pith always clearly septate; bark variable.
        49. Calyx glabrous on abaxial surface; pedicels glabrous; corolla 8.5–13 mm long; leaves entire; bark furrowed, corky; [Mexico]. ..... 7. *A. sleumeri.*
        49. Calyx sparsely to moderately pubescent on abaxial surface; pedicels sparsely to moderately pubescent; corolla 6.5–9.5 mm long; leaves entire or serrate; bark very shallowly furrowed, not corky; [SE United States]. ..... 8. *A. populifolia.*

45. Leaves of single plant varying from ovate to elliptic or oblong (rarely obovate), apex acute- or rounded-mucronate to acuminate.
    50. Capsules roughened/warty; leaves with apex acute- or rounded-mucronate to acuminate, margin convex-curved to ± straight when viewed from above; [SE Brazil].
        51. Leaves ovate to elliptic (rarely oblong), margin very slightly revolute from base to near apex; [Guanabara, Rio de Janeiro]. ..... 24. *A. uleana.*
        51. Leaves ovate to elliptic/oblong, usually at least few per plant ± parallel sided, margin plane to very slightly revolute at base only; [Rio Grande do Sul to Paraná]. ..... 23. *A. niederleinii.*
    50. Capsules ± smooth; leaves with apex elongate-mucronate to short-acuminate, margin convex-curved when viewed from above; [chiefly N South America]. ..... 4. *A. duckei.*

44. Inflorescence axis to 3–15 cm long.
    52. Inflorescence axis with hairs to 0.15–0.4 mm long, straight to curved; calyx lobes 0.7–1.8 mm long; corolla (3.7–)4–9 mm long; leaves thinly coriaceous, flexible when dry; [N Andes]. ..... 1. *A. albiflora.*
    52. Inflorescence axis glabrous or with hairs to 0.05–0.15 mm long, curved; calyx lobes 1–2.7 mm long; corolla 6.5–11 mm long; leaves thickly coriaceous, rather inflexible when dry; [SE Brazil]. ..... 9. *A. coriifolia.*

Agarista D. Don ex G. Don sect. **Agarista**

Leucothoë D. Don sect. *Agastia* DC. Prodr. 7: 603. 1839. *Leucothoë* D. Don subg. *Agarista* (D. Don ex G. Don) Drude *in* Engler & Prantl, Nat. Pflanzenfam. **4**(1): 42. 1889. LECTOTYPE SPECIES: *Agarista nummularia* (Cham. & Schldl.) G. Don.

Agarista D. Don ex G. Don sect. *Leucothoides* Niedenzu, Bot. Jahrb. **11:** 186. 1890. LECTOTYPE SPECIES: *Agarista serrulata* (Cham.) G. Don (= *Agarista chlorantha* (Cham.) G. Don).

Agarista D. Don ex G. Don sect. *Euagarista* Niedenzu, Bot. Jahrb. **11:** 186. 1890, nomen illegit.

Twigs with nonchambered to clearly chambered, *Calluna*-type pith. Leaves with abaxial epidermis nonpapillose, adaxial epidermis usually tall with divided cells (see Stevens, 1970). Style usually swollen toward apex. Capsules with placentae subapical to ± central; seeds 0.5–3(–3.5) mm long.

NUMBER OF SPECIES (TAXA): 29 (35).

1. **Agarista albiflora** (B. Fedtsch. & Basilevsk.) Judd, comb. nov.

FIGURE 2, d.

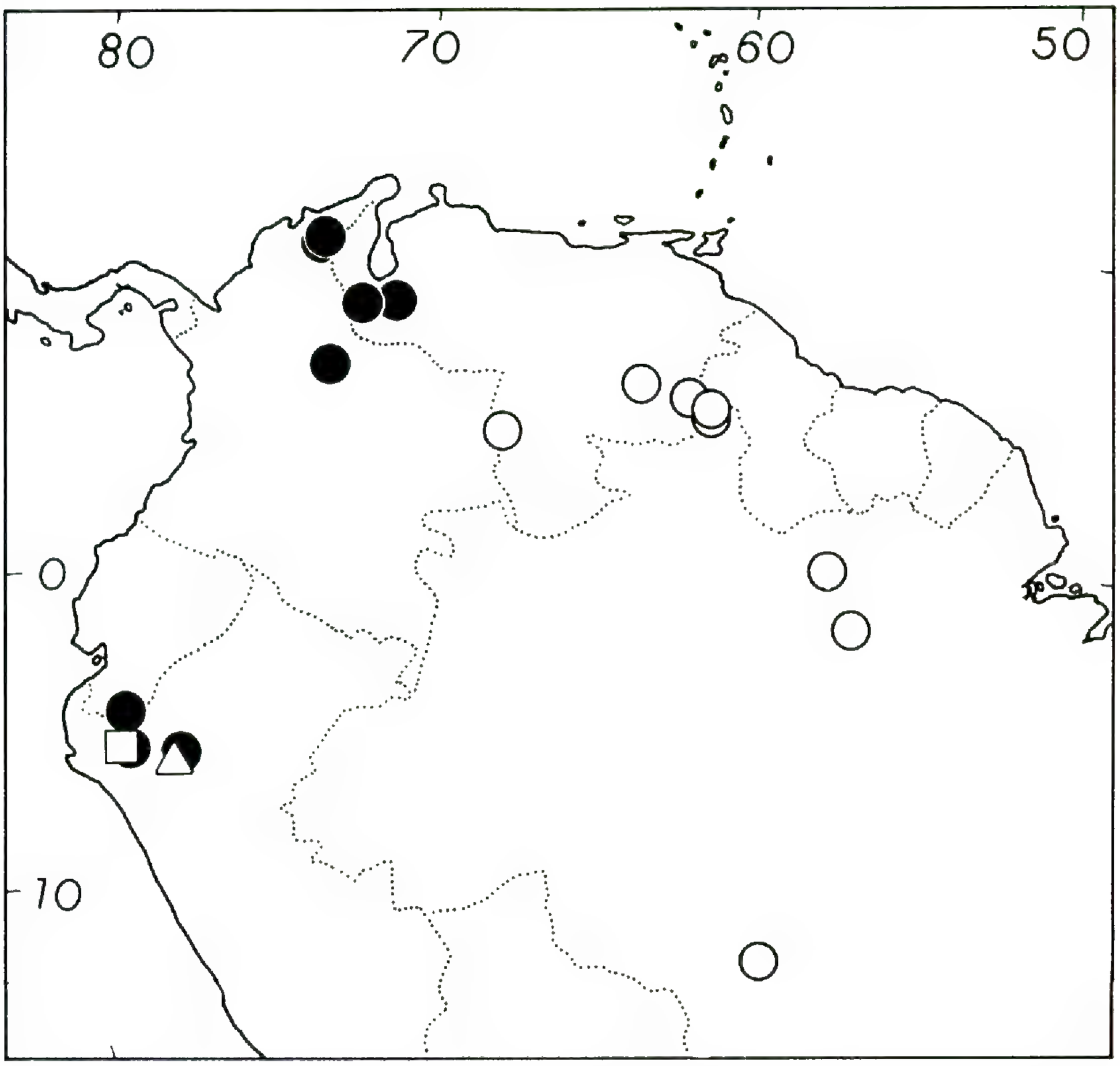
Leucothoë albiflora B. Fedtsch. & Basilevsk. Not. Syst. Herb. Hort. U.S.S.R. **6:** 23. 1926. TYPE: Colombia, Boyacá, near Soatá, April 1843, *Linden 1322* (holotype, LE; isotypes, BR, F!, G, K!, NY!, P!, US!, W).

Leucothoë columbiana Sleumer, Notizbl. Bot. Gart. Berlin **12:** 479. 1935. TYPE: Colombia, Magdalena, Sierra Nevada de Santa Marta, "El Manon," ca. 2100 m alt., 26 Feb. 1928, *Schultze 1113* (holotype, B (destroyed)).

Leucothoë andina Sleumer, *ibid.* 478. TYPE: Peru, Amazonas, Pipos, E of Chachapoyas, 2000 m alt., 19 July 1904, *Weberbauer 4362* (holotype, B (destroyed); isotypes, NY(fragment)!, USM).

Shrub to 3 m tall. Twigs with or without scattered gland-headed hairs, otherwise moderately pubescent, with ± nonchambered pith. Buds to ca. 1.5 mm long. Leaves alternate; petiole 2–8 mm long; blade revolute in bud, ovate to elliptic, 1.6–7 by 0.8–2.7 cm, flat to slightly (strongly) abaxially curved, coriaceous, the apex acute- to rounded-mucronate, the base widely cuneate to cordate, the margin entire (slightly undulate), plane to very slightly (strongly) revolute, the adaxial surface with or without gland-headed hairs on midvein, otherwise sparsely to moderately pubescent on midvein (also sparsely pubescent on lamina and along margin), the abaxial surface with or without gland-headed hairs on midvein, otherwise very sparsely to moderately pubescent on midvein, usually with few to many inconspicuous glandular dots along midvein. Inflorescences axillary racemes to 3–10 cm long, the axis with or without scattered gland-headed hairs, otherwise sparsely to moderately pubescent. Pedicels 2–7.5 mm long, with or without gland-headed hairs, otherwise moderately pubescent; bracteoles 2, opposite to subopposite, basal or nearly so, narrowly triangular, to ca. 0.8 mm long; bracts to 1 mm long. Calyx lobes triangular with acuminate apices, 0.7–1.8 by 0.6–1.1 mm, abaxial surface sparsely to moderately pubescent; corolla cylindrical to urceolate-cylindrical, 4–9 by 2–3.5 mm, white (red tinged at tip, or red), abaxially glabrous; filaments 2.5–5 mm long, anthers 1–1.5 mm long; ovary sparsely to densely pubescent. Capsules

FIGURE 2. a, b, *Agarista mexicana* var. *pinetorum:* a, *Williams & Molina 14000*; b, *Villarreal de Puga 4761,* abaxial leaf surface light due to dense layer of unicellular hairs. c, *A. revoluta* (*Rose & Russell 20687*). d, *A. albiflora* (*Jorgensen & Prieto JP-55*). Scale = 2 cm.



MAP 2. Distribution of *Agarista albiflora* (dots), *A. subcordata* (triangle), *A. bracamorensis* (square), and *A. duckei* (circles).

subglobose to short-ovoid, 3–5.5 by 4–7.5 mm, placentae subapical; seeds 1.5–2 mm long.

DISTRIBUTION AND ECOLOGY. Northern Andes from Venezuela and Colombia south to Peru (MAP 2). Moist montane forests, dwarf forests, rocky areas with scattered shrubs; 1800–2500 m alt. Flowering April to September.

REPRESENTATIVE SPECIMENS. **Colombia.** BOYACÁ: Villa de Leiva, La Candelaria, *Cleef 359* (L). MAGDALENA: San Sebastian de Rabago, *Romero-Castañeda 867* (COL). **Venezuela.** MÉRIDA: San Antonio, *Jahn 1086* (US); Pueblo Nuevo, *López-Palacios 768* (NY). TÁCHIRA: above La Grita, slopes below Páramo de la Negra, *Steyermark 57108* (A, F). **Ecuador.** LOJA: Hacienda Guaycopamba on Río Guaycopamba, 22 km S of Vilcabamba, *Fosberg & Giler 23072* (COL, NY, US); W slope of Cordillera Condor, Huilcabamba, NW of Nudo de Sabinilla, 54 km S of Loja, *Jorgensen & Prieto Jp-55* (FLAS, NY, S). **Peru.** CAJAMARCA: Jaén, El Parco, *Friedberg 665* (L).

Agarista albiflora, a taxon that is rather variable in leaf size and shape, and in the degree to which the margins are revolute, is probably most closely related to *A. subcordata* and *A. bracamorensis.* It can be distinguished from the former

by its often larger leaves and its inflorescence axes with usually elongated, straight to curled, unicellular hairs, and from the latter by its much larger, usually nonrevolute leaves and its often longer pedicels. *Agarista albiflora* may also be confused with *A. revoluta* and *A. duckei,* or *A. mexicana, A. sleumeri,* and *A. populifolia* (see key for distinguishing characters).

Agarista albiflora and *A. subcordata* may be slightly sympatric since both have been collected in the Chachapoyas region; the mechanisms isolating these two very similar species are in need of field study.

2. **Agarista subcordata** (Dunal) Judd, comb. nov.

Gaylussacia subcordata Dunal *in* DC. Prodr. **7:** 557. 1839. *Leucothoë subcordata* (Dunal) Sleumer, Bot. Jahrb. **78:** 461. 1959. TYPE: Peru, Amazonas, Chachapoyas, *Matthews s.n.* (holotype, G; fragment and photo of holotype, F!; isotypes, E!, K!, S!).

Shrub. Twigs sparsely to very sparsely pubescent, with ± nonchambered pith. Buds to ca. 1.8 mm long. Leaves alternate; petiole 1–2.5 mm long; blade revolute in bud, ovate to elliptic, 1–3.1 by 0.6–1.3 cm, flat to slightly abaxially curved, coriaceous, the apex acute- to rounded-mucronate, the base rounded to slightly cordate, the margin entire (slightly undulate), the adaxial surface glabrous to sparsely pubescent on midvein, the abaxial surface glabrous to sparsely pubescent on midvein, often with few to several inconspicuous glandular dots along midvein. Inflorescences axillary racemes to 5–10 cm long, axis sparsely to moderately pubescent. Pedicels 3.5–7 mm long, sparsely to moderately pubescent; bracteoles 2, at or near base to within lower ⅓ of pedicel, narrowly triangular, to ca. 1.1 mm long; bracts to 1.5 mm long. Calyx lobes triangular with acuminate apices, 1–1.5 by 0.9–1.5 mm, the abaxial surface glabrous to very sparsely pubescent, especially near base; corolla cylindrical to urceolate-cylindrical, 6–7.5 by 3–3.5 mm, white, abaxially glabrous; filaments ca. 3.5 mm long, anthers ca. 1.3 mm long; ovary glabrous to very sparsely pubescent near apex. Capsules subglobose to short-ovoid, 4–5 by 5.5–6.5 mm, placentae subapical; seeds not seen.

DISTRIBUTION. Andes, endemic to Chachapoyas region of northern Peru, ca. 2700 m alt. (MAP 2).

REPRESENTATIVE SPECIMENS. **Peru.** AMAZONAS: Chachapoyas, Guancas, *Matthews 1635* (E, GH, K, P); Chachapoyas, *Williams 7549* (F).

The poorly known *Agarista subcordata* is probably closely related to both *A. albiflora* and *A. bracamorensis.* All three taxa are limited to the northern Andes, but *A. albiflora* is by far the most widely distributed. *Agarista subcordata* can be readily distinguished from *A. albiflora* by its often smaller leaves and its inflorescence axis with short, curled hairs, and from *A. bracamorensis* by its wider, less strongly revolute leaves and its longer pedicels.

3. **Agarista bracamorensis** (Humb., Bonpl., & Kunth) G. Don, Gen. Syst. **3:** 837. 1834.

Andromeda bracamorensis Humb., Bonpl., & Kunth, Nov. Gen. Sp. Pl. **3:** 225. *t. 263.* 1818. *Leucothoë bracamorensis* (Humb., Bonpl., & Kunth) DC. Prodr. **7:** 603. 1839.

TYPE: Peru, Cajamarca, prov. Bracamora, near S. Felipe and Páramo de Yamoca, ca. 2350 m, *Bonpland 3564* (holotype, P!; fragment and photo of holotype, F!).

Shrub or small tree. Twigs sparsely pubescent, with obscurely chambered pith. Buds to ca. 0.5 mm long. Leaves alternate; petiole 1.5–4 mm long; blade revolute in bud, ovate, 0.8–1.5 by 0.25–0.7 cm, moderately abaxially curved, coriaceous, the apex acute-mucronate, the base rounded, the margin entire, strongly revolute, the adaxial surface sparsely pubescent on midvein, the abaxial surface essentially glabrous, often with few inconspicuous glandular dots along midvein. Inflorescences axillary racemes to ca. 5 cm long, axis sparsely to moderately pubescent. Pedicels 1.5–3 mm long, sparsely to moderately pubescent; bracteoles 2, opposite, nearly basal, narrowly triangular, to ca. 0.6 mm long; bracts to 1 mm long. Calyx lobes triangular with acute to acuminate apices, 0.5–1.5 by 0.4–0.6 mm, abaxial surface glabrous; corolla ± cylindrical, 4.5–6 by 2–3.5 mm, white, abaxially glabrous; filaments ca. 3.5 mm long, anthers ca. 1.3 mm long; ovary glabrous. Capsules short-ovoid, 4–4.5 by 4.5–5.5 mm, placentae subapical; seeds ca. 1.5–2 mm long.

DISTRIBUTION. Andes, northern Peru, Bracamora region, ca. 2350 m alt. (MAP 2).

REPRESENTATIVE SPECIMENS. Known only from type collection.

This rare and little-known species is probably closest to *Agarista albiflora* and *A. subcordata,* two other Andean species. It is readily separated from these allies by its very small, strongly revolute leaves. It is also superficially similar to the revolute-leaved Brazilian species *A. organensis, A. chlorantha, A. hispidula,* and *A. ericoides* but is quickly distinguished from all of them by its combination of round-based leaves, short pedicels, and short calyx lobes.

4. **Agarista duckei** (Huber) Judd, comb. nov.

Leucothoë duckei Huber, Bull. Soc. Bot. Genève, II. **1:** 246. *fig. 1.* 1909. TYPE: Brazil, Pará, in campis arenosis ad ripam orient. fl. Yamundá, pr. Faro, 27 Aug. 1907, *Ducke 8526* (holotype, MG; fragment and photo of holotype, F!; isotype, G-Boiss.).
Leucothoë venezuelensis A. C. Smith, Contr. U. S. Natl. Herb. **29:** 335. 1950. TYPE: Venezuela, Bolívar, Gran Sabana, Cerro Akurimá, 20 March 1946, *Tamayo 3236* (holotype, US!; photo of holotype, NY!; isotype, F!).

Shrub to tree to 6 m tall, with roughly furrowed bark. Twigs sparsely to densely pubescent, with nonchambered pith. Buds to ca. 1.5 mm long. Leaves alternate; petiole 2–6(–7) mm long; blade revolute in bud, elliptic to slightly ovate (obovate), (1.5–)2–5.7 by 0.5–2.1 cm, nearly flat to strongly abaxially curved, coriaceous, the apex elongate-mucronate to short-acuminate, the base narrowly to widely cuneate or rounded, the margin entire, plane to strongly revolute, the adaxial surface sparsely pubescent on midvein, especially proximal portion (with few scattered hairs on proximal portion of lamina), the abaxial surface sparsely to moderately pubescent on midvein, with few to several very inconspicuous glandular dots along midvein. Inflorescences axillary racemes to 0.5–1.5 cm long, axis densely pubescent. Pedicels 2.5–12 mm

long, moderately to densely pubescent; bracteoles 2, alternate, from nearly basal to within lower ⅓ of pedicel, triangular to narrowly so, to ca. 1.2 mm long; bracts to 1.2 mm long. Calyx lobes triangular with acuminate apices, 0.9–2.3 by 0.7–1 mm, abaxial surface moderately to densely pubescent; corolla urceolate to cylindrical, 6–8 by 3–4.5 mm, white (rarely pink), abaxially glabrous; filaments 3.5–4.7 mm long, anthers 0.9–1.1 mm long; ovary sometimes with scattered gland-headed hairs, otherwise sparsely to densely pubescent. Capsules ovoid to globose or subglobose, 5–6 by 6–8 mm, valves rarely white bordered, placentae subapical; seeds 1.5–3 mm long.

DISTRIBUTION AND ECOLOGY. Southern Venezuela and western Pará and Mato Grosso, Brazil (MAP 2). Thickets and forests on sand, open sandy areas, bush forest and savannas on white sand, river and lake margins, rocky slopes and plateaus; ca. 100–1400 m alt. Flowering May through August (October and December).

REPRESENTATIVE SPECIMENS. **Brazil.** MATO GROSSO: Sararé, Radambrasil, *Pires & Santos 16397* (FLAS, NY). PARÁ: E of Faro, *Ducke 5708* (NY, P, S, US; photos, F, GH); Monte Alegre, Alto de Serra do Ereré, *Lima 53-1609* (K). **Venezuela.** AMAZONAS: Sabanito Morocoto, right bank of Río Orinoco, 2 km below mouth of Río Atabapo, *Wurdack & Adderley 42692* (F, GH, NY, UC, US, VEN). BOLÍVAR: Gran Sabana, Canaima Lagoon, Avensa Camp, *Ehrendorfer 74103-1b* (VEN); Canaima, *López-Palacios 3029* (L, NY); Canaima, between hotel and airport, *Steyermark 106370* (F, MO, NY, VEN); Carretera El Dorado to Santa Elena de Uairén, km 198 S of El Dorado, plateau above Lamá-merú, *Steyermark et al. 106642* (VEN); top of rocky slope, *Steyermark et al. 106634* (NY).

The closest relative of *Agarista duckei* seems to be the geographically separated *A. revoluta* (see MAP 5). The strong similarities between the two species were also noted by Sleumer (1959). In both species the leaf blade is often strongly to moderately abaxially curved. *Agarista duckei* is readily distinguished from *A. revoluta* by its shorter inflorescences, its short-acuminate to elongate-mucronate leaf apices, and its usually white flowers. *Agarista duckei* is also related to (and may sometimes be confused with) the Andean species *A. albiflora*; see key for distinguishing characters.

Albert C. Smith (1950) distinguished *Leucothoë venezuelensis* (populations in Venezuela) from *L. duckei* (populations in state of Pará, Brazil) on the bases of petiole length, leaf shape and base, calyx-lobe apex, and corolla shape. However, the variation in these characters is so slight that separating the plants into two species is quite arbitrary. Thus, the two are considered to be conspecific. The large disjunction separating the Mato Grosso population from similar plants in southern Venezuela is puzzling. Additional localities probably exist; more collecting is evidently needed.

The pollen morphology of this species (Venezuelan populations) has been studied by Maguire, Steyermark, and Luteyn (1978).

5. **Agarista revoluta** (Sprengel) J. D. Hooker ex Niedenzu, Bot. Jahrb. **11**: 236. 1889.

Shrub or small and often gnarled tree to 3(–6) m tall, with roughly furrowed bark. Twigs sparsely to densely pubescent, with nonchambered pith. Buds to

ca. 1.1 mm long. Leaves alternate; petiole 2–7 mm long; blade revolute in bud, ovate to elliptic, 1.3–4.5 by 0.5–2.2 cm, slightly to strongly abaxially curved (rarely nearly flat), coriaceous, the apex obtuse- to retuse-mucronate (rarely acute-mucronate), the base rounded (to very slightly cordate), the margin entire, slightly to strongly revolute, the adaxial surface sparsely to moderately pubescent on proximal portion of midvein (with few hairs on adjacent portion of lamina); abaxial surface sparsely pubescent on midvein or only on proximal portion, or densely pubescent on lamina and midvein, with few inconspicuous glandular dots along midvein. Inflorescences axillary racemes to (1–)1.5–6.5 cm long, axis moderately to densely pubescent. Pedicels 3–11 mm long, sparsely to densely pubescent; bracteoles 2, opposite to alternate, from basal to near midpoint of pedicel, narrowly triangular, to ca. 1 mm long; bracts to 1.3 mm long. Calyx lobes triangular with acuminate apices, 0.9–1.6 by 0.6–1.5 mm, abaxial surface sparsely to densely pubescent; corolla ± cylindrical, 6–9 by 3.5–5 mm, red to white, abaxially glabrous or with very few unicellular hairs near apex to moderately pubescent; filaments 4.5–5.5 mm long, anthers 1–1.2 mm long; ovary very sparsely to densely pubescent. Capsules ovoid to short-ovoid or subglobose, 4–5.5 by 5–7 mm, valves often slightly white bordered, placentae subapical; seeds 2–3.5 mm long.

DISTRIBUTION. Southeastern Brazil, along coast from Bahia south to Estado do Rio.

KEY TO THE VARIETIES OF AGARISTA REVOLUTA

1. Abaxial surface of lamina glabrous, but sparsely pubescent on midvein, especially proximal portion; corolla glabrous or with very few unicellular hairs near apex. . . . . 5a. var. *revoluta*.
1. Abaxial surface of lamina densely pubescent; corolla moderately pubescent, especially near apex. . . . . 5b. var. *velutina*.

5a. **Agarista revoluta** (Sprengel) J. D. Hooker ex Niedenzu var. **revoluta**

FIGURE 2, C.

Andromeda revoluta Sprengel, Neue Entdeck. **2:** 131. 1821. *Agarista sprengelii* G. Don, Gen. Syst. **3:** 837. 1834, nomen superfl. *Leucothoë revoluta* (Sprengel) DC. Prodr. **7:** 604. 1839. *Leucothoë revoluta* (Sprengel) DC. var. *sellowii* Meissner *in* Martius, Fl. Brasil. **7:** 160. 1863, nomen superfl. TYPE: Brazil, Estado do Rio, Restinga de Cabo Frio, *Sellow s.n.* (holotype, B (destroyed); isotype at B! selected as lectotype; remaining isotypes, BM!, BR, E!, G, K!, L!, M!, P!, W; photos of isotype, F!, G, GH!).

Andromeda crassifolia Nees, Flora **4:** 297. 1821. TYPE: Brazil, Estado do Rio, Cabo Frio, *Neuwied 13, 14* (not seen, probably at BR, GOET; see Sleumer, 1959).

Leucothoë bahiensis DC. var. *salzmannii* DC. Prodr. **7:** 604. 1839 (= *L. bahiensis* var. *bahiensis*; chosen as nominate variety by Sleumer, 1959). *Leucothoë revoluta* (Sprengel) DC. var. *salzmannii* (DC.) Meissner *in* Martius, Fl. Brasil. **7:** 160. 1863. TYPE: Brazil, Bahia, 1830, *Salzmann 314* (lectotype, G; isolectotypes, NY(fragment)!, P!; unnumbered Salzmann collections, possible isolectotypes, G, GH!, K!, MO!; photos of unnumbered Salzmann collection, F!, G, GH!).

Leucothoë bahiensis DC. var. *blanchetii* DC. Prodr. **7:** 604. 1839. *Leucothoë revoluta* (Sprengel) DC. var. *blanchetii* (DC.) Meissner *in* Martius, *ibid.* TYPE: Brazil, Bahia, Monte Cerrato, *Blanchet 1680* (holotype, G; isotypes, F!, K!, P!, W).

Andromeda nitida Vell. Conc. Fl. Flum. 174. 1825, a later homonym of *A. nitida* Bartram ex Marsh. Arbust Am. 8. 1785 = *Lyonia lucida* (Lam.) K. Koch. *Leucothoë bahiensis* DC. var. *arrabidae* DC. Prodr. 7: 604. 1839. *Leucothoë revoluta* (Sprengel) DC. var. *arrabidae* (DC.) Meissner *in* Martius, Fl. Brasil. 7: 160. 1863. TYPE: lectotype here designated as illustration in Vell. Conc. Fl. Flum. ic. **4:** *t. 94.* 1835.

Twigs sparsely to densely pubescent. Leaves with adaxial surface sparsely pubescent on proximal portion of midvein; abaxial surface sparsely pubescent on midvein, especially proximal portion, otherwise glabrous. Pedicels 3–8.5 mm long, sparsely to densely pubescent. Calyx lobes with abaxial surface sparsely to densely pubescent. Corolla abaxially glabrous or with very few unicellular hairs near apex. Ovary very sparsely to sparsely pubescent.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, along coast from southern Bahia south to Estado do Rio (MAP 5). Coastal scrub on wet to dry sand (sometimes intermixed with sedge meadows), sand dunes; near sea level (rarely inland to 1000 m alt.). Flowering July through October.

REPRESENTATIVE SPECIMENS. **Brazil.** BAHIA: Santa Cruz Cabrália, *Belém & Pinheiro 2544* (C, L, NY); Pôrto Seguro, *Duarte 6144* (L, M, NY, US); between Alcobaça and Caravelas on BA 001, 20 km S of Alcobaça, *Harley 18047* (NY); 7 km NW of Mucuri, *Mori et al., Herb. Cent. Pesquisas do Cacau 10474* (NY). ESTADO DO RIO: Itapuã, *Athayde III-1961* (L); Macahé, Restinga de Cabiuna, *Brade 15781* (B); Cabo Frio, *Duarte & Pereira 5793* (L, S, US); Cabo Frio, along st. to town at jct. with rd. to Arraial do Cabo, *Lems 640317* (M, MO, NY, US); S of Cabo Frio, *Lindeman 6330* (L); Macahé, near Cabo Frio, *Riedel 494* (G, GH, GOET, K, L, NY, S); Arraial do Cabo, Pontal Beach, *Segadas-Vianna et al. I-470* (L); Casimiro de Abreu Co., dist. of Barra de São João, 5 km N of Rio das Ostras, *Segadas-Vianna et al. I-949* (L); Restinga de Itaipu, *Sucre 7611* (NY); Restinga de Cabo Frio, *Ule 4752* (HBG). MINAS GERAIS: Serra Sapucaí, municipio de Jequitinhonha, *Magalhães 17459* (L).

5b. **Agarista revoluta** (Sprengel) J. D. Hooker ex Niedenzu var. **velutina** Judd, var. nov.

Varietas haec ab Agarista revoluta var. revoluta differt in foliis cum pagina abaxiali dense velutina, pedicellis longioribus, corollis et ovariis pubescentibus.

Twigs densely pubescent. Leaves with adaxial surface sparsely to moderately pubescent on midvein and adjacent lamina; abaxial surface velutinous on lamina and midvein. Pedicels 6–11 mm long, densely pubescent. Calyx lobes with abaxial surface densely pubescent. Corolla abaxially moderately pubescent, especially near apex. Ovary ± densely pubescent.

TYPE. Brazil, Bahia, municipio do Salvador, Dunas do Abaeté, 29 Aug. 1976, *J. Silva Araújo et al. 49* (holotype, NY!; isotype, CEPEC).

DISTRIBUTION AND ECOLOGY. Eastern Brazil, on coast near Salvador, Bahia (MAP 5). Coastal scrub. Flowering August and September.

REPRESENTATIVE SPECIMENS. Known only from type collection.

Agarista revoluta, a distinct species with variably revolute, moderate-sized, obtuse- to retuse-mucronate leaves, is probably allied to the geographically

separated *A. duckei* (see MAP 2). It is readily distinguished by its longer inflorescences and its more abruptly and shortly mucronate leaves. Some individuals of *A. albiflora,* an Andean species, may be confused with *A. revoluta*; however, the former taxon has leaves that are usually less abruptly mucronate and only infrequently revolute, inflorescence hairs that are longer, and capsule valves that are never bordered.

Agarista revoluta is divided here into two geographically isolated varieties (MAP 5) separable primarily by the indumentum on the abaxial leaf surface. Variety *velutina,* discovered only recently, may be more widespread, and further collecting is needed along the coast of Bahia.

This taxon is unique in that it is the only species of *Agarista* known to occur in coastal "restingas."

6. **Agarista mexicana** (Hemsley) Judd, Jour. Arnold Arb. **60:** 495. 1979.

Shrub or tree to 8(–11) m tall, with thick, corky, deeply furrowed bark. Twigs very sparsely to densely pubescent, with nonchambered to clearly chambered pith. Buds to ca. 1.5 mm long. Leaves alternate (to subopposite or nearly 3-whorled at some nodes); petiole 2–12.5 mm long; blade revolute in bud, ovate, 2–7.5(–9) by 0.8–2.5(–3.2) cm, flat, coriaceous, the apex acuminate, the base narrowly cuneate to rounded, the margin entire (slightly undulate), plane to very slightly revolute near base, the adaxial surface glabrous to densely pubescent on midvein (with few unicellular hairs on proximal portion of lamina); abaxial surface essentially glabrous to densely pubescent on midvein, otherwise glabrous to densely pubescent, with few to several inconspicuous glandular dots along midvein. Inflorescences (fasciclelike) axillary racemes to 0.5–2.5(–4) cm long, axis sparsely to densely pubescent. Pedicels 2–8 mm long, very sparsely to densely pubescent; bracteoles 2, alternate to opposite, from nearly basal to within lower ⅓ (rarely to midpoint) of pedicel, triangular to narrowly so, to ca. 0.9 mm long; bracts to 1 mm long. Calyx lobes triangular with acuminate apices, 0.9–1.8 by 0.5–2 mm, abaxial surface very sparsely to densely pubescent; corolla cylindrical, 6–9.5 by 2.5–5 mm, white, abaxially glabrous to sparsely pubescent (especially near apex); filaments 4.5–6 mm long, anthers 1–1.8 mm long; ovary very sparsely to densely pubescent. Capsules subglobose to short-ovoid, 3–4.5(–5) by 5–7 mm, placentae subapical; seeds 1.5–2.7 mm long.

DISTRIBUTION. Mountainous areas of Mexico and Central America, from Veracruz and Jalisco south to Honduras and El Salvador.

COMMON NAMES. Cachimbo (Honduras, see Standley & Williams, 1952); quemanote, pellejo de lagarto, nacahuite (Mexico).

KEY TO THE VARIETIES OF AGARISTA MEXICANA

1. Abaxial surface of lamina glabrous to occasionally sparsely pubescent, hairs not obscuring abaxial epidermis. ..... 6a. var. *mexicana.*
1. Abaxial surface of lamina densely to occasionally moderately pubescent, hairs ± obscuring epidermis. ..... 6b. var. *pinetorum.*

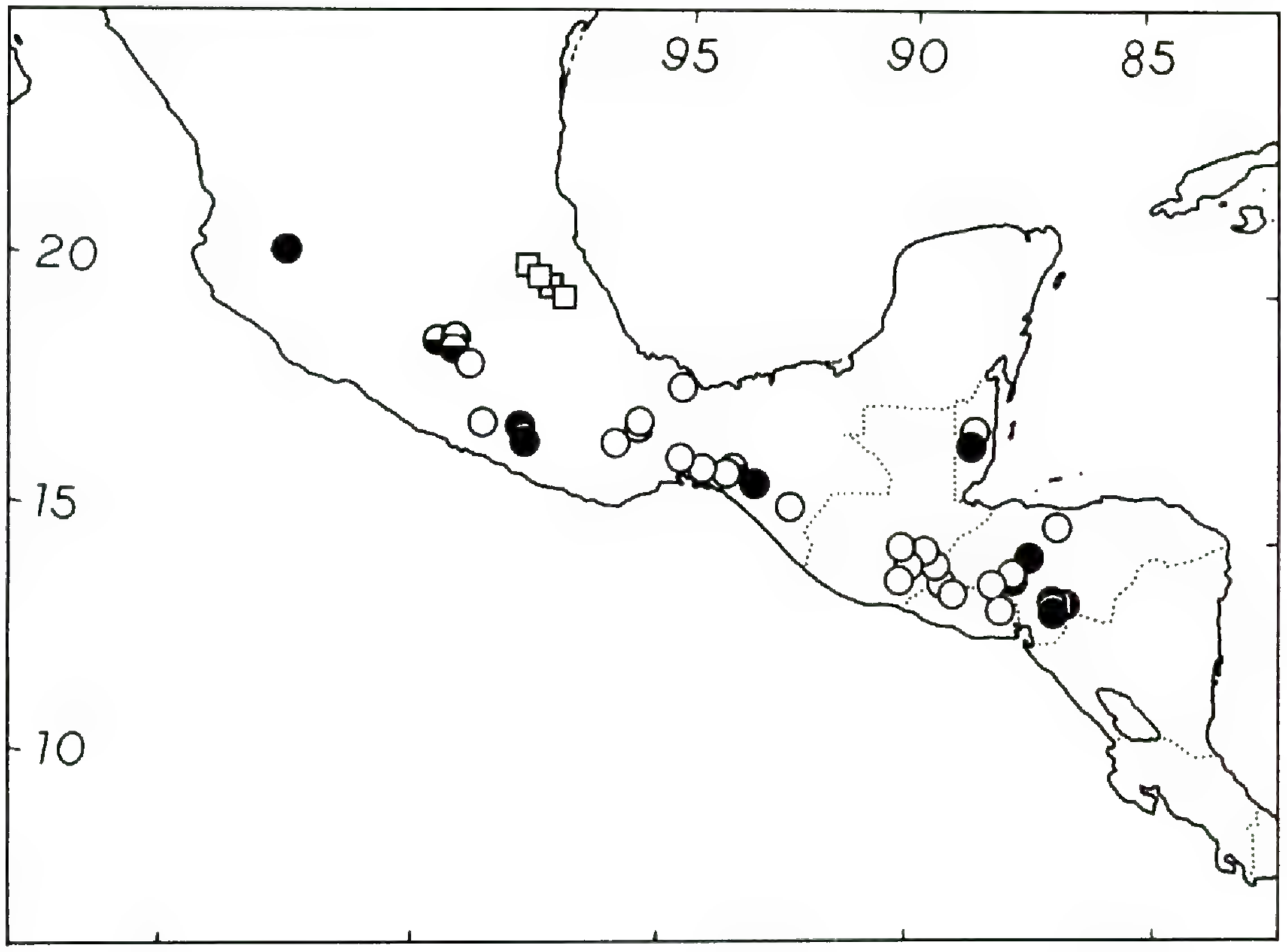
6a. **Agarista mexicana** (Hemsley) Judd var. **mexicana**

Andromeda mexicana Hemsley, Biol. Centr.-Am. Bot. **2:** 282. 1881. *Leucothoë mexicana* (Hemsley) Small, N. Am. Fl. **29:** 57. 1914. TYPE: Mexico, Oaxaca, Sierra San Pedro Nolasco, *Jürgensen 866* (holotype, K; isotype, G!).

Twigs very sparsely to densely pubescent. Leaf blades with abaxial surface glabrous to occasionally sparsely pubescent, epidermis not obscured. Ovary very sparsely to densely pubescent.

DISTRIBUTION AND ECOLOGY. Mountainous areas of Mexico and Central America, from states of México, Guerrero, Oaxaca, and Veracruz south to Honduras and El Salvador (MAP 3). Dry ridges, *Pinus* and/or *Quercus* forests, *Pinus, Quercus,* and *Liquidambar* forests with *Ulmus, Zinowiewia, Weinmannia,* and *Styrax,* montane mixed forests, disturbed openings, and forest margins; frequently in sandy soil; 170–2500 m alt. Reported from forests of *Pinus teocote, P. rudis,* and *P. oocarpa* by Gómez-Pompa (1973). Flowering mid-February through April (early May).

REPRESENTATIVE SPECIMENS. **Mexico.** CHIAPAS: SE of Cerro Baul on border with Oaxaca, 16 km NW of Rizo de Oro, municipio de Cintalapa, *Breedlove & Smith 31375* (MEXU, MO); SW of Tal-tenango, along rd. to Finca Pousia, *Miranda 6945* (MEXU, US). GUERRERO: Agua de Obispo, near 17°20′N, 99°34′W, *Kruse 630* (ENCB, MEXU); Taxco, *Miranda 3074* (MEXU). MÉXICO: dist. Temascaltepec, Guayabal, *Hinton 3377* (GH, NY, US); Nanchititla, *Hinton 3415* (GH, NY, US); Temascaltepec, *Hinton 3528* (GH, NY, UC, US); dist. Sultepec, Almoloya, *Hinton et al. 7450* (BM, F, G, GH, MO, NY, US); Cerro de Mamatla, Zacualpan, *Matuda 30563* (F, MEXU); Puerto del Embocadero, 7 km W of Luvianos, municipio de Tejupilco, *Rzedowski 22122* (WIS). OAXACA: Zempoaltepetl, between Santa María and Mitla, *Camp 2761* (GH, NY, S, UC); Chavela, *Mell 14* (F, NY, US); dist. Choapam, Yaveo, trail to Arroyo Culebras, *Mexia 9157* (B, F, G, GH, MO, NY, S, UC, US); Teotalcingo to Choapan, *Reko 4080* (US); Choapan to Comaltepec, *Reko 4116* (US); between Río Grande and Niltepec, *Xolocotzi X-1230 & Sharp 46232* (GH, MEXU). VERACRUZ: Cerro Monte de Oro, *Dorantes et al. 856* (F, MEXU); Falda del Cerro Azul, transecto Punta Limon–Cerro Azul, *Dorantes et al. 1114* (MEXU); along trail to Santa Marta, 2 km N of San Fernando, municipio Soteapan, *Nee et al. 24729* (F, FLAS); Ocozotepec, 6 km NW of Soteapan, *Sousa 3253* (F, MEXU); 1 km SW of Ocozotepec, *Sousa 3532* (F, MEXU). **Belize:** Hidden Valley Falls Rd., *Poppleton s.n.,* 26 Dec. 1973 (FLAS). **Guatemala:** Zamorora, dept. Santa Rosa, *Heyde & Lux 4530* (F, G, GH, NY, US); Sierra de las Minas, near San Gerónimo, dept. Baja Verapaz, *Kellerman 6636* (F, US); above Morazán, El Progreso, *Sharp 4633* (GH, MEXU); between Finca San José and Montaña Nube, 1.5 mi SE of Concepción de las Minas, dept. Chiquimula, *Steyermark 30857* (F, NY); Montaña Castilla, vic. of Montaña Cebollas, 3 mi SE of Quezaltepeque, dept. Chiquimula, *Steyermark 31303* (F); Sierra de las Minas, dept. Zacapa, Volcán de Monos, *Steyermark 42317* (F, NY); Sierra de las Minas, near Finca Piamonte, dept. El Progreso, *Steyermark 43427* (F, NY); Aguacate, dept. Jalapa, *Williams 13172* (F, GH); near Soledad, dept. Jalapa, *Williams 14239* (F). **Honduras:** dept. Comayagua, near Siguatepeque, *Allen 6219* (F); dept. Intibuca, Cascada de Yamaranguilla, *Molina 6362* (F); dept. Yoro, above Los Flores, vic. of Coyoles, *Yuncker et al. 8172* (BM, F, G, GH, NY, US). **El Salvador:** dept. Chalatenango, La Reina, *Calderón* (F, US); dept. Santa Ana, Cerro Miramundo, NE of Metapán, *Carlson 956* (F, UC); dept. Chalatenango, S of La Palma, *Lagos & Weberling 256* (L, M); dept. Morazán, easternmost peak, Montes de Cacaguatique, lat. 13°46′N, long. 88°13′W, *Tucker 698* (G, NY, P, UC, US).



MAP 3. Distribution of *Agarista mexicana* var. *mexicana* (circles), *A. mexicana* var. *pinetorum* (dots), and *A. sleumeri* (squares). Localities with both *A. mexicana* var. *mexicana* and intermediates between this taxon and var. *pinetorum* indicated by half-closed circles.

6b. **Agarista mexicana** (Hemsley) Judd var. **pinetorum** (Standley & Williams) Judd, Jour. Arnold Arb. **60:** 495. 1979. FIGURE 2, a, b.

Leucothoë pinetorum Standley & Williams, Ceiba **3:** 54. 1952. *Leucothoë mexicana* (Hemsley) Small var. *pinetorum* (Standley & Williams) Sleumer, Bot. Jahrb. **78:** 466. 1959. TYPE: Honduras, El Paraíso, Manzaragua, 1400 m alt., 4 April 1948, *Williams & Molina 14000* (holotype, US!; photos of holotype, F!, GH!, NY!, UC!; isotypes, GH!, MEXU!, MO!, US!).

Twigs moderately to densely pubescent. Leaf blades with abaxial surface densely (to moderately) pubescent, epidermis obscured or nearly so. Ovary moderately to densely pubescent.

DISTRIBUTION AND ECOLOGY. Mountainous areas of Mexico (states of Jalisco, Guerrero, and Chiapas), Belize, and Honduras (MAP 3). Rocky, brushy hillsides, *Pinus* and/or *Quercus* forests, *Pinus* savannas, *Pinus, Quercus,* and *Liquidambar* forests, and montane mixed forests; often in sandy soil; 500–2000 m alt. Flowering March through April (early May).

REPRESENTATIVE SPECIMENS. **Mexico.** CHIAPAS: E base of Cerro Tres Picos near Cerro Bola, logging rd. SW of Colonia Agronomos Méxicanos, municipio Villa Corzo, *Breedlove & Thorne 30037* (DUKE, ENCB, F, MEXU, MO). GUERRERO: Mina, Manchon dist., *Hinton 10082* (C, F, G, GH, M, MO, NY, UC); Armenia-Zoyate, Mina, *Hinton 10159* (C, ENCB, F,

G, GH, M, MO, NY, UC, US); Chilacayote–La Soledad, Mina, *Hinton et al. 14199* (F, GH, MO, NY, UC, US); Petlacala, Mina, *Hinton 14205* (F, MO, NY, US). JALISCO: La Venta, municipio de Zapopan, *Diáz-Luna 87* (ENCB); Venta del Astillero, La Primavera, *Villarreal de Puga 150* (ENCB); Sierra de la Venta, 18 km W of Guadalajara, *Villarreal de Puga 531* (ENCB). **Belize:** Augustine, 16°34′N, 88°54′W, *Hunt 438* (BM, US); El Cayo dist., 17 km S of Georgeville, *Liesner & Dwyer 1612* (MO, NY); El Cayo dist., San Agustín, *Lundell 6792* (F, NY, US). **Honduras:** Las Jagnas, Minas de Oro, Comayagua dist., *Edwards P-180* (A); El Paraíso, rd. from Zamoras to Güinope, *Webster et al. 11988* (F, GH, MO, US); dept. Morazán, Rd. Valle de Angeles near San Antonio, *Molina 389* (F, GH, MEXU, MO, UC, US); dept. El Paraíso, between Galeras and Las Casitas, *Molina 10765* (F, US); dept. Comayagua, La Piramide, *Molina 14393* (F); dept. Morazán, San Antonio de Oriente, *Rodríguez 3133* (F, GH, NY); dept. El Paraíso, NW of Güinope, *Standley et al. 2047* (F, NY, US); dept. Morazán, vic. of Agua Amarilla, *Standley 12297* (F); dept. El Paraíso, above Galeras, *Williams & Molina 10246* (F, GH); dept. Comayagua, 5 km N of Siguatepeque, *Williams & Molina 18128* (F, GH, US).

Agarista mexicana is closely allied to *A. sleumeri* and *A. populifolia*; all three species are characterized by ovate leaves with acuminate apices and rounded to cuneate bases, and by short inflorescences of white flowers. *Agarista mexicana* can be differentiated from both taxa by its pubescent ovary, from *A. populifolia* by its corky, prominently furrowed bark, and from *A. sleumeri* by its pubescent calyx and pedicels and its smaller corollas and leaves.

Agarista mexicana is a widely distributed taxon (see MAP 3) that is extremely variable in its unicellular indumentum. Populations of this species are here divided into two weakly differentiated geographic varieties on the basis of the density of unicellular hairs on the abaxial leaf surface. However, some populations are variable in leaf pubescence, and intermediate specimens are known, mostly in the state of México. Representative intermediate material includes:

Mexico. CHIAPAS: near Fenia, *Purpus 294* (US); E of Monserrate, *Purpus 10156* (A, F), *Purpus 10518* (A, NY). MÉXICO: dist. Temascaltepec, Ypericones, *Hinton 3899* (GH, NY, US); 5 km SW of Nanchititla, Tejupilco, *Medrano et al. 5030* (MEXU); Puerto del Embocadera, 7 km W of Luvianos, municipio de Tejupilco, *Rzedowski 22122* (ENCB, MEXU); La Cienaga, 4 km S of Sultepec, *Rzedowski 30392* (ENCB).

Agarista mexicana var. *mexicana* has been illustrated by Standley and Williams (1952, *fig. 30*).

7. **Agarista sleumeri** Judd, sp. nov. FIGURE 3, a.

Frutex vel arbor ad 6(–20) m alta. Ramuli hornotini glabri cum medulla septata. Folia ovata, 4–11.5(–13) cm longa, 1.6–4.5(–5.3) cm lata, coriacea, ad apicem acuminata, ad basin cuneata vel rotundata; margo ± planiuscula, integra; pagina abaxialis glabra; petioli 6.5–13 mm longi. Inflorescentiae axillares, racemosae, ad 0.5–2.5(–4) cm longae; axis glaber vel leviter pubescens. Pedicelli glabri, 3.5–8.5 mm longi. Flores 5-merus. Calyx lobis 1.2–2.6(–3) mm longis, 0.7–2 mm latis, abaxialiter glabris. Corolla cylindrica, 8.5–13 mm longa, 3–7.5 mm lata, alba, abaxialiter glabra. Filamenta 5–7.5 mm longa; antherae 1.3–1.7 mm longae. Ovarium glabrum. Capsula subglobosa vel brevissime ovoidea, 3–4.5 mm longa, 5–8 mm lata, placentis subapicalibus. Semina 1.5–2.4 mm longa.

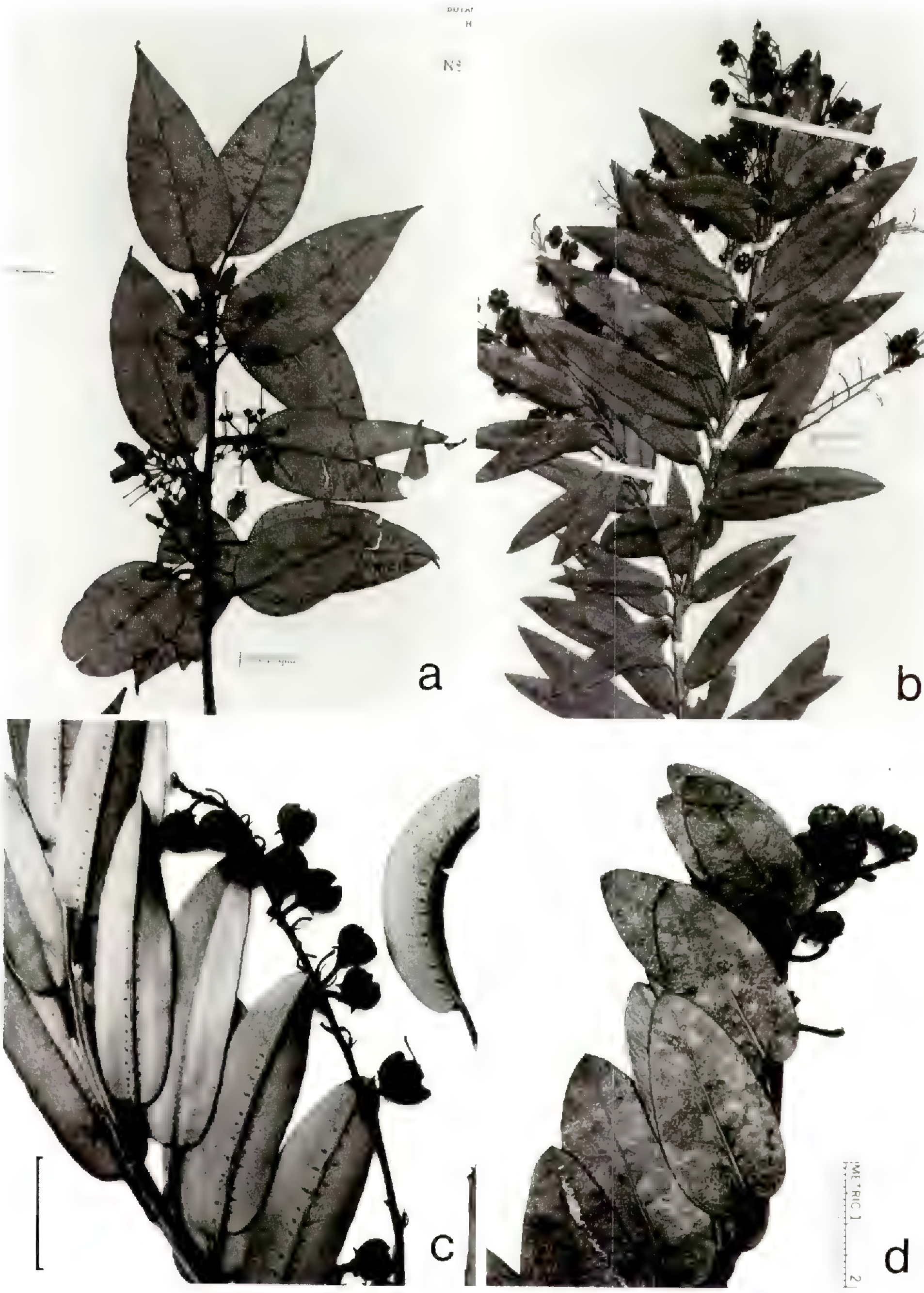


FIGURE 3. a, *Agarista sleumeri* (*Koch & Garcia 76103*). b, *A. oleifolia* var. *oleifolia* (*Glaziou 15171*). c, *A. coriifolia* var. *bradei* (*Irwin et al. 28486*): note round-based leaves with conspicuous glandular dots extending along midvein on abaxial surface. d, *A. coriifolia* var. *coriifolia* (*Duarte 2044*): note cordate-based leaves with glandular dots less well developed. Scale = 2 cm.

Shrub or tree to 6(–20) m tall, with corky, longitudinally furrowed bark. Twigs glabrous, with clearly chambered pith. Buds to ca. 1.2 mm long. Leaves alternate (to rarely subopposite at few nodes); petiole 6.5–13 mm long; blade revolute in bud, ovate, 4–11.5(–13) by 1.6–4.5(–5.3) cm, flat, coriaceous, the apex acuminate, the base cuneate to rounded, the margin entire (slightly undulate), plane to very slightly revolute near base, the adaxial surface glabrous to very slightly pubescent near extreme proximal portion of midvein, the abaxial surface glabrous, with few to several inconspicuous glandular dots along midvein. Inflorescences (fasciclelike) axillary racemes to 0.5–2.5(–4) cm long, axis essentially glabrous to sparsely pubescent. Pedicels 3.5–8.5 mm long, glabrous; bracteoles 2, alternate, nearly basal to within lower ¼ of pedicel, triangular to narrowly so, to ca. 0.8 mm long; bracts to 1.3 mm long. Calyx lobes triangular with acuminate apices, 1.2–2.6(–3) by 0.7–2 mm, abaxial surface glabrous; corolla cylindrical, 8.5–13 by 3–7.5 mm, white, abaxially glabrous; filaments 5–7.5 mm long, anthers 1.3–1.7 mm long; ovary glabrous. Capsules subglobose to short-ovoid, 3–4.5 by 5–8 mm, placentae subapical; seeds 1.5–2.4 mm long.

TYPE. Mexico, Hidalgo, municipio de Tenango de Doria, 30 km NE of Tulancingo, rd. between Metepec and Tenango de Doria, 19 km N of Metepec, 22 May 1976, *S. D. Koch & J. García P. 76103* (holotype, ENCB!; isotypes, MEXU!, MO!).

DISTRIBUTION AND ECOLOGY. Mexico, limited to small area of Hidalgo, Veracruz, and Puebla in Sierra Madre Oriental (MAP 3). *Pinus* and/or *Quercus* forests, *Pinus* and *Liquidambar* forest, mixed forest of *Pinus, Quercus, Alnus,* or *Cupressus*, and *Lyonia* and *Cupressus* forest; 1220–2250 m alt. Flowering April and May (June).

REPRESENTATIVE SPECIMENS. **Mexico.** HIDALGO: 2 km SW of Tutotepec, *Gimante 608* (ENCB); municipio de Tenango de Doria, El Estribo, *Gimante 950* (ENCB, MEXU, WIS); NE of Honey, *Hernandez 767* (MEXU); municipio de Tenango de Doria, 25 km NE of Tulancingo, *Perino 3353* (NY); border of Hidalgo and Veracruz, Puente Agapito Barranco, *Gómez-Pompa 4354* (F, GH). PUEBLA: N of Tlatlanqui, *Boege 1713* (MEXU); Necaxa, *Miranda 3421* (MEXU); Pahuatlán, *Miranda 3641* (MEXU); along Río Tenango, near Tenango, *Sharp 45353* (MEXU); 1 km from Tlaxpanaloya, Naupan, *Vela 455* (ENCB). VERACRUZ: La Capilla, 3 km from Huayacocotla, *Calzada & Horritz 2628* (F, MEXU, NY); SW entrance to Huayacocotla on rd. from Palo Bendito, *Diggs & Nee 2957* (F, FLAS); El Paraje, Huayacocotla, *Hernandez & Cedillo 817* (F, GH, MEXU, MO); municipio Huayacocotla, *Hernandez 1150* (MEXU); between La Cruz del Ataque and Zacualpan, *Vela 618* (ENCB).

Agarista sleumeri is most closely related to *A. populifolia* and *A. mexicana,* differing from both in its abaxially glabrous calyx and glabrous pedicel (vs. very sparsely to densely pubescent calyx and pedicel) and its larger corolla. It can also be distinguished from the latter species by its glabrous (vs. very sparsely to densely pubescent) ovary, its clearly septate pith, and its usually larger leaves. These three species form a well-marked subgroup of the genus and can be separated from the South American species by their ovate leaves with cuneate

FIGURE 4. *Agarista populifolia* (*Judd 2609*): a, segment of twig, × .5; b, longitudinal section of twig, showing chambered pith, × 2; c, cross section of older stem, showing hollow central portion, × 1; d, margin of leaf, × 10; e, multiseriate-stalked, gland-headed hair of pedicel, × 130; f, unicellular hairs of pedicel, × 130; g, flower, × 5; h, stamen, × 10; i, anther, × 25; j, capsule and portion of pedicel, × 5; k, columella with placentae, × 6.5; l, seed with elongated testa cells, × 10.

to rounded bases and acuminate apices, their white flowers, and their short racemes. The three species are geographically isolated (MAPS 3, 4).

It is a pleasure to name this distinctive species for Dr. H. Sleumer, who has done so much to increase our taxonomic understanding of *Agarista* and various other ericad groups.

8. **Agarista populifolia** (Lam.) Judd, Jour. Arnold Arb. **60:** 195. 1979.
FIGURE 4.

Andromeda populifolia Lam. Encycl. Méth. Bot. **1:** 159. 1783. *Andromeda laurina* Michaux, Fl. Bor.-Am. **1:** 253. 1803, nomen superfl. *Lyonia populifolia* (Lam.) K. Koch, Dendrol. **2:** 123. 1872. *Leucothoë populifolia* (Lam.) Dippel, Handb. Laubh. **1:** 356. 1889. TYPE: United States, South Carolina, *Fraser s.n.* (holotype, P-LA; photo of holotype, GH!).

Andromeda lucida Jacq. Collect. **1:** 95. 1786, non *Andromeda lucida* Lam. Encycl. **1:** 157. 1783 (= *Lyonia lucida* (Lam.) K. Koch).

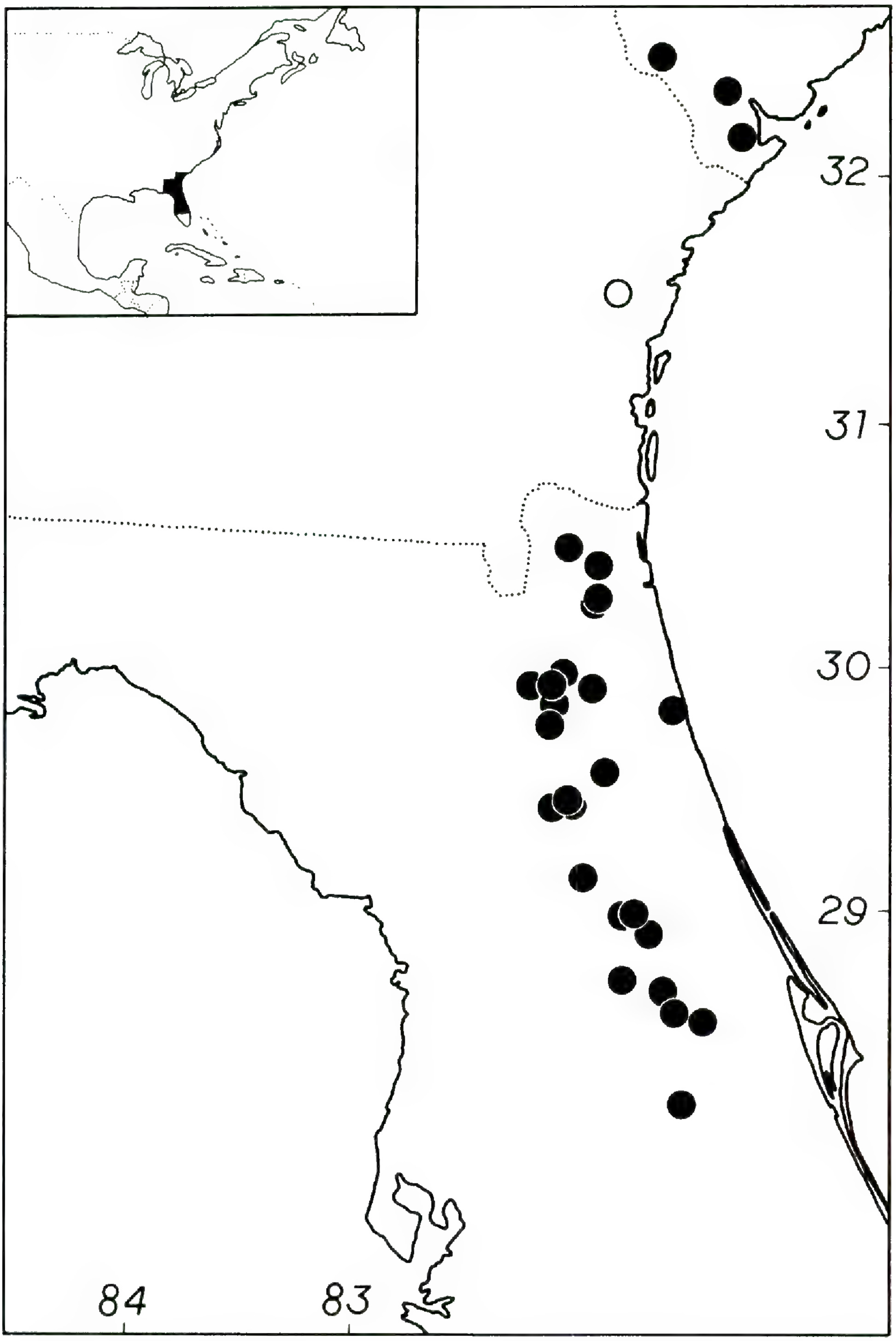
Andromeda reticulata Walter, Fl. Carolin. 137. 1788. TYPE: not seen.

Andromeda acuminata Aiton, Hortus Kew. **2:** 70. 1789. *Andromeda acuminata* Lodd. ex C. F. Ludwig, Neue Wilde Baumz. 4. 1783, nomen nudum. *Leucothoë acuminata* (Aiton) G. Don, Gen. Syst. **3:** 832. 1834. TYPE: cultivated, "introduced by Mr. John Cree" (not seen).

Andromeda formosissima Bartram, Travels N. S. Carol. **5:** 24, 172, 303. 1791, nomen nudum.

Shrub or small tree to 7 m tall, with shallowly furrowed bark. Twigs with or without scattered gland-headed hairs, otherwise glabrous to sparsely pubescent, with clearly chambered pith. Buds to ca. 1 mm long. Leaves alternate; petiole 3–12 mm long; blade revolute in bud, ovate, 2.6–9(–11.2) by 0.9–4(–5) cm, flat, coriaceous, the apex acuminate (to nearly acute), the base narrowly cuneate to rounded, the margin entire to obscurely or sharply serrate (serrations, when present, each associated with gland-headed hair) (undulate), plane to very slightly revolute near base, the adaxial surface with or without scattered gland-headed hairs, otherwise sparsely pubescent on midvein, especially proximal portion, the abaxial surface with or without gland-headed hairs along midvein (and proximal portion of lamina), otherwise glabrous or with very few unicellular hairs at base of midvein, with few to several inconspicuous glandular dots along midvein. Inflorescences (fasciclelike) axillary racemes to 1–2.5(–3.5) cm long, the axis with or without scattered gland-headed hairs, otherwise sparsely to densely pubescent. Pedicels 5.5–11.5 mm long, with or without gland-headed hairs, otherwise sparsely to moderately pubescent; bracteoles 2 (rarely 3), alternate, nearly basal to within lower ⅓ (rarely to midpoint) of pedicel, triangular or narrowly so, to ca. 1.2 mm long, very rarely subtending an axillary flower; bracts to 1.2 mm long. Calyx lobes triangular with acuminate apices, 0.9–2 by 0.6–1.5 mm, the abaxial surface with or without gland-headed hairs, otherwise sparsely to moderately pubescent; corolla cylindrical, 6–9.5 by 3–5 mm, white, abaxial surface glabrous; filaments 4–5.5 mm long, anthers 1.1–1.4 mm long; ovary glabrous. Capsules subglobose to short-ovoid, 3–4 by 4.5–6.5 mm, placentae subapical; seeds 1.4–2 mm long. $2n = 24$ (Wood, 1961).

DISTRIBUTION AND ECOLOGY. Southeastern U. S. Atlantic Coastal Plain from southern South Carolina to eastern Florida (MAP 4). Acidic swamps in pine



MAP 4. Distribution of *Agarista populifolia* (open circle = unspecified Georgia locality).

flatwoods, mixed hydric hammocks (hardwood swamps) of *Fraxinus, Quercus, Nyssa, Sabal, Acer, Liquidambar, Persea, Gordonia, Carpinus,* and *Pinus,* riverine swamps, swamp forests of *Taxodium* or *Chamaecyparis* (along with various hardwoods), bayheads and lake margins, frequently along streams or in ravines; near sea level to 55 m alt. Flowering chiefly late March through early May.

COMMON NAMES. Pipe-plant, pipe-stem wood.

REPRESENTATIVE SPECIMENS. **United States.** FLORIDA. Clay Co.: ravine at Goldhead Branch St. Park, NE of Keystone Heights, *Arnold s.n.,* 5 May 1940 (FLAS); Rte. 21, 4.8 mi N of jct. with Rte. 16, along Mill Creek, S22, T5S, R24E, *Judd 2541* (FLAS); 5 mi W of Penny Farms, S15, T6S, R24E, *Ward 5521* (FLAS). Duval Co.: near Jacksonville, *Curtiss 1692* (A, G, GH, K, M, MO, NY, UC, US). Lake Co.: Alexander Springs, *Ford & West s.n.,* 11 July 1958 (FLAS, UNC). Marion Co.: just N of Orange Springs, near jct. of Orange Creek and Rte. 21, S25, T11S, R23E, *Judd 2609* (FLAS, FSU, GH, MO, S, UNC); Juniper Springs, *Murrill s.n.,* 5 May 1940 (FLAS, MO). Nassau Co.: near Callahan, *E. J. Palmer 38293* (A, MO, S). Orange Co.: Rock Springs, S15, T20S, R28E, *Moore s.n.,* 1 April 1961 (FLAS, MO, UNC). Osceola Co.: near Kissimmee, *Hunnewell 8707* (GH). Putnam Co.: S1, T11S, R24E, center of section, *Cooper 697* (FLAS). Seminole Co.: 5 mi W of Oviedo, S23, T21S, R30E, *Lotspeich & Perkins 472* (FLAS). St. Johns Co.: near St. Augustine, *Reynolds s.n.,* May–June 1875 (MO, NY). GEORGIA: without definite locality, *Le Conte s.n.* (MO); *Feay s.n.* (NY). SOUTH CAROLINA. Beaufort Co.: Bluffton, *Mellichamp s.n.,* 1876 (GH, NY). Hampton Co.: Garnett, *Lawton s.n.,* 28 Sept. 1931 (NCU). Jasper Co.: Elliott (1817) reported it from near the "Black Swamp, on the road from Coosawhatchie to the Sisters Ferry."

Agarista populifolia, the northernmost-ranging species of the genus, is very closely related to *A. sleumeri.* The two species are distinguished by calyx and pedicel indumentum, corolla size, and bark characters, and they are geographically separated, with *A. populifolia* occurring on the Atlantic Coastal Plain from South Carolina to Florida and *A. sleumeri* in the Sierra Madre Oriental of Hidalgo, Veracruz, and Puebla. *Agarista populifolia* is also allied with *A. mexicana,* from which it is easily distinguished by its glabrous (vs. pubescent) ovary, its shallowly (vs. corky and prominently) furrowed bark, and its more consistently septate pith. It is puzzling that *A. populifolia* has consistently been misclassified despite the many characters linking it to its South and Central American relatives (see TABLE 1).

Agarista populifolia is rather variable in glandular indumentum and in the size and margin of the leaves. Leaves of some plants are sharply (to obscurely) serrate, while those of others are entire; the two forms are commonly found intermixed within the populations. In addition, some plants have gland-headed hairs on the inflorescences and frequently also on the stems and/or leaves, while others completely lack them. Most populations contain plants with such hairs and plants without them.

This species is locally common in eastern Florida (MAP 4) from Osceola County to Nassau County but is apparently extremely rare in Georgia and South Carolina. In fact, the presence of the taxon in Georgia is somewhat questionable since no exact localities are known, although Bartram (1791)

reported it growing along the St. Marys River. The species is occasionally cultivated (Ingram, 1961, *fig. 26*; Melvin, 1981).

Andromeda serratifolia (see DC. Prodr. **7**: 602, 609. 1839) and *A. serrata* (see *ibid.* 602) are horticultural names (of no nomenclatural standing) that were occasionally used for *Agarista populifolia* in the late eighteenth or early nineteenth century.

9. **Agarista coriifolia** (Thunb.) J. D. Hooker ex Niedenzu, Bot. Jahrb. **11**: 236. 1889.

Shrub (to tree) to 2(–5) m tall. Twigs glabrous to moderately pubescent (glaucous), with nonchambered to clearly chambered pith. Buds to ca. 1.8 mm long. Leaves alternate to subopposite or nearly 3-whorled at some nodes; petiole 2–18 mm long; blade revolute in bud, ovate to elliptic or oblong, 1.8–10.5 by 0.6–3.5(–5) cm, ± flat, very coriaceous, the apex acute- to rounded-mucronate to acuminate, the base cordate to cuneate, the margin entire, plane (slightly revolute near base, rarely slightly undulate), the adaxial surface glabrous to sparsely pubescent on midvein, especially proximal portion, the abaxial surface glabrous to very sparsely pubescent along proximal portion of midvein, with glandular dots absent, or few to many and inconspicuous to conspicuous along midvein. Inflorescences axillary or terminal racemes or panicles, to (2.5–)4.5–28 cm long, axis glabrous to densely pubescent. Pedicels 2–14 mm long, glabrous to densely pubescent; bracteoles 2 (rarely to 4), alternate to opposite, from nearly basal to near middle of pedicel, triangular to narrowly so, to ca. 1.6 mm long; bracts to 4 mm long. Calyx lobes triangular with acuminate apices, 1–2.7 by 0.6–2.2 mm, abaxial surface glabrous to sparsely (moderately) pubescent; corolla cylindrical to urceolate-cylindrical, 6.5–11 by 3–6.5 mm, white or greenish white to red, abaxially glabrous (rarely with very few unicellular hairs near apex); filaments 4–6 mm long, anthers 1.3–2.3 mm long; ovary glabrous to moderately pubescent. Capsules short-ovoid to subglobose, 3–6 by 4.5–8 mm, placentae subapical (rarely ± central); seeds 1–2.6 mm long.

DISTRIBUTION. Eastern Brazil, Bahia, Minas Gerais, and Estado do Rio.

KEY TO THE VARIETIES OF AGARISTA CORIIFOLIA

1. Leaves usually ovate (to ± elliptic), base usually cordate to rounded, abaxial surface with glandular dots lacking to limited to proximal half of blade; calyx lobes abaxially glabrous to sparsely (moderately) pubescent. ..... 9a. var. *coriifolia*.
1. Leaves ± oblong to slightly elliptic (slightly ovate), base usually cuneate to rounded, abaxial surface with glandular dots usually extending along midvein to near apex of blade; calyx lobes abaxially glabrous. ..... 9b. var. *bradei*.

9a. **Agarista coriifolia** (Thunb.) J. D. Hooker ex Niedenzu var. **coriifolia**

FIGURE 3, d.

Andromeda coriifolia Thunb. Pl. Brasil. Decas 1, p. 9. 1817. *Leucothoë coriifolia* (Thunb.) DC. Prodr. 7: 605. 1839. TYPE: Brazil, Minas Gerais, Villa Rica, *Freyreiss s.n.* (holotype, UPS).

Leucothoë neriifolia Cham. & Schldl. Linnaea **1**: 522. 1826. *Agarista neriifolia* (Cham. & Schldl.) G. Don, Gen. Syst. **3**: 838. 1834. *Leucothoë laxiflora* Meissner var. *sellowii*

Meissner *in* Martius, Fl. Brasil. **7:** 157. 1863 (= var. *laxiflora*), nomen superfl. TYPE: Brazil, Minas Gerais, without definite locality, *Sellow s.n.* (holotype, B (destroyed); fragment of holotype, NY; photos of holotype, F!, G!, GH!; isotypes, E!, K!).

Andromeda crassifolia Pohl, Pl. Brasil. **2:** 34. 1828/29, non Nees, Flora **4:** 297. 1821. *Agarista pohlii* G. Don, Gen. Syst. **3:** 837. 1834, nomen novum. *Leucothoë crassifolia* (Pohl) DC. Prodr. **7:** 605. 1839. *Leucothoë crassifolia* (Pohl) DC. var. *subevenia* Meissner *in* Martius, Fl. Brasil. **7:** 158. *t. 59, fig. 1.* 1863 (= var. *crassifolia*), nomen superfl. *Leucothoë pohlii* (G. Don) Sleumer, Bot. Jahrb. **78:** 463. 1959. TYPE: Brazil, Minas Gerais, Diamantina, Pico Itambé, Nov. 1821, *Pohl 3506* (holotype, W; fragment of holotype, NY!).

Leucothoë laxiflora Meissner var. *martii* Meissner *in* Martius, Fl. Brasil. **7:** 157. 1863. TYPE: Brazil, Estado do Rio, near Paraiba, *Martius 1118* (holotype, M!; fragment of holotype, NY!; photos of holotype, F!, GH!; isotypes, M!).

Leucothoë laxiflora Meissner var. *subcordata* Meissner *in* Martius, *ibid.* TYPE: not seen.

Leucothoë laxiflora Meissner var. *hookeriana* Meissner *in* Martius, *ibid.* 158. TYPE: cultivated in England, in garden of Mr. Cunningham (see Hooker & Smith, 1851, *t. 4593*) (holotype, K!).

Leucothoë crassifolia (Pohl) DC. var. *subreticulata* Meissner *in* Martius, *ibid.* TYPE: Brazil, Minas Gerais, Itambé, Aug. 1840, *Martius 836* (holotype, M!; fragment of holotype, NY!; isotypes, BR, G!, K!, P!, W; photos of isotype, F!, GH!).

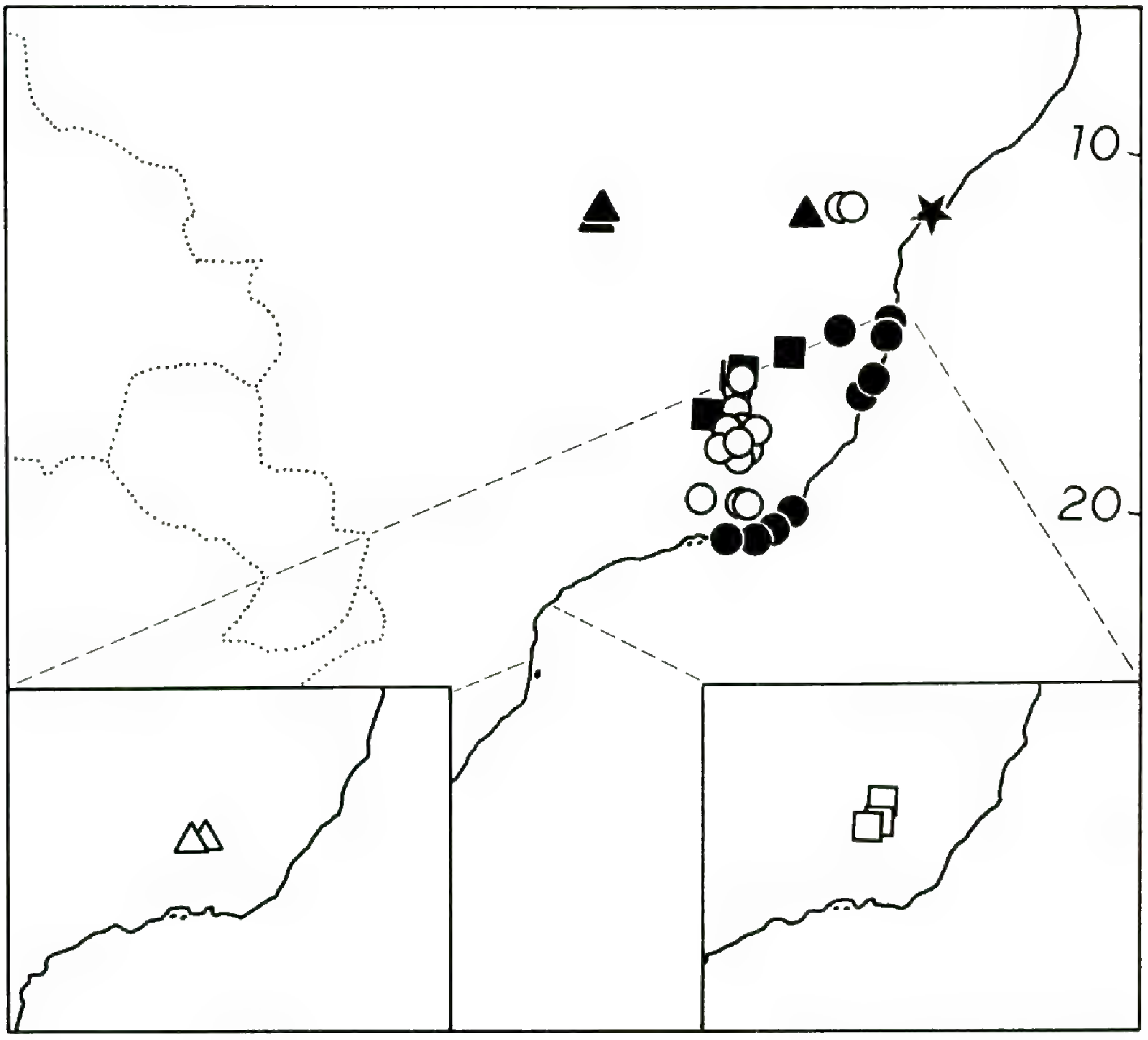
Leucothoë crassifolia (Pohl) DC. var. *reticulata* Meissner *in* Martius, *ibid.* TYPE: Brazil, Minas Gerais, without definite locality, *Claussen 535* (holotype, BR; fragment of holotype, NY!).

Leucothoë crassifolia (Pohl) DC. var. *macrophylla* Meissner *in* Martius, *ibid.* TYPE: Brazil, Serra da Paraca, fl. Paraiba, *Martius s.n.* (holotype, M!; photos of holotype, F!, GH!).

Shrub (or tree) to 2(–5) m tall. Twigs glabrous to moderately pubescent. Leaves with petiole 2–18 mm long; blade ovate (to ± elliptic), 1.8–10.5 by (0.6–)1–3.5(–5) cm, base usually cordate to rounded, abaxial surface with glandular dots absent to limited to proximal half. Inflorescence axis to 6–28 cm long, glabrous to densely pubescent. Pedicels glabrous to densely pubescent. Calyx lobes abaxially glabrous to sparsely (or moderately) pubescent; corolla 6.5–10.5 mm long, red to white; ovary glabrous to sparsely pubescent.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, from Bahia to southern Minas Gerais and adjacent Estado do Rio (MAP 5). Open rocky and/or grassy campo, open scrub, thickets and forests, frequently along streams; usually in sandy soil, with sandstone or manganese outcrops; 500–1950 m alt. Flowering chiefly June through September (to January or February).

REPRESENTATIVE SPECIMENS. **Brazil.** BAHIA: Lençóis, *Duarte 9337* (L); Serra do Sincorá, by Rio Cumbuca, ca. 3 km S of Mucugê, *Harley et al. 15911* (E, L, MO, NY, US); 10 km S of Andaraí on rd. to Mucugê, *Harley 18758* (NY); 3 km S of Mucugê, *Mori et al. 12578* (NY); between Lençóis and Itaberaba, *Pereira 2040* (L); Serra do Sincorá, *Ule 7336* (HBG, L). MINAS GERAIS: E slopes of Pico do Itambé, *Anderson et al. 35887* (C, F, L, NY, US); Serra do Taquaril, Belo Horizonte, *Barreto 528* (F); Serra do Cipó, km 131, Palacio, Santa Luzia, *Barreto 9253* (F); Cachoeira do Campo, *Claussen 54* (G); Palmeira, Rio Carandaí, *Duarte 4314* (L); Caraça, *Emygdio et al. 3525* (NY); Furnas, Alvinópolis, *Emygdio et al. 3588* (NY); Ribeirão das Capidalas, *Emygdio 3623* (NY); Diamantina, *Gardner 4990* (E, G, GH, K, NY, P, US); Serra do Palmital, near São Bartholomeu, *Glaziou 15172* (C, K, L, P); Serra do Itacolomy, *Gomes 2846* (F); Pico Itambé, São Antonio do Itambé, *Hatschbach 30123* (C, L, MO, UC); Serra do Caraça, *Irwin et al. 29067* (L, MO,



MAP 5. Distribution of *Agarista coriifolia* var. *coriifolia* (circles), *A. coriifolia* var. *bradei* (solid squares), *A. pulchra* (open squares), *A. subrotunda* (open triangles), *A. chapadensis* (solid triangles), *A. revoluta* var. *revoluta* (dots), and *A. revoluta* var. *velutina* (star).

NY), *St.-Hilaire s.n.*, 1816–1821 (P); Serra do Cipó, Mato Dentro, *Macedo 3757* (NY, S, US); Serro Frio, *Martius s.n.* (M); Serra do Curral d'El Rey, *Reinhardt s.n.*, Sept. 1855 (C); Serra d'Uro Branco, *St.-Hilaire 234* (P); Itambé, *St.-Hilaire 395* (P); Serra do Ouro Prêto, *Ule s.n.*, Feb. 1892 (HBG); Casa Branca, Ouro Prêto, *Williams 8130* (GH).

9b. **Agarista coriifolia** (Thunb.) J. D. Hooker ex Niedenzu var. **bradei** (Sleumer) Judd, comb. et stat. nov. FIGURE 3, c.

Leucothoë bradei Sleumer, Notizbl. Bot. Gart. Berlin **13:** 213. 1936. TYPE: Brazil, Minas Gerais, Diamantina, June 1934, *Brade 13614* (holotype, RB; fragment of holotype, LIL; photos of isotype, B (destroyed), S!).

Shrub to 2 m tall. Twigs glabrous to very sparsely pubescent. Leaves with petiole 4–11 mm long; blade ± oblong to slightly elliptic (slightly ovate), (2.4–)3–7.5 by 0.6–2.5(–3) cm, base usually cuneate to rounded, abaxial surface with glandular dots usually extending along midvein from base to near apex. Inflorescence axis to (2.5–)4.5–15(–20) cm long, glabrous to sparsely pubescent.

Pedicels glabrous to sparsely pubescent. Calyx lobes abaxially glabrous; corolla 8–11 mm long, red; ovary glabrous to moderately pubescent.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, Minas Gerais (MAP 5). Rocky or grassy campo, shrubby cerrado, gallery forest, sometimes on termite mounds; ca. 1200–1410(?) m alt. Flowering September and October.

REPRESENTATIVE SPECIMENS. **Brazil.** MINAS GERAIS: Serra do Espinhaço, 13 km SW of Rio Jequiti and Mendanha, on rd. to Diamantina, *Anderson 8992* (C, F, L, MO, NY); between Diamantina and Guinda, *Archer 4103* (A, NY); Diamantina, *Duarte 8927* (L); Guinda, Diamantina, *Hatschbach 27371* (C, L, NY, S, UC, US); 27 km SW of Diamantina on rd. to Gouveia, *Irwin et al. 22043* (F, L, NY); 3 km N of São João da Chapada, rd. to Campo do Sampaio, *Irwin 28486* (F, L, NY); Chapada, *St.-Hilaire, Cat. B[1], n. 2048* (P).

Agarista coriifolia is probably closely related to *A. pulchra* and *A. subrotunda*. It can be separated from the former by its larger, narrower leaves with a length/width quotient of (1.5–)1.8–6 (vs. 0.9–1.7) and its glabrous to densely pubescent inflorescence axes, and from the latter by its abaxially glabrous leaves. This species may also be confused with *A. pulchella* var. *pulchella* or *A. oleifolia* (both varieties), but these taxa have more or less central placentae and usually less coriaceous leaves that always lack conspicuous abaxial glands (see key for other distinguishing features).

Agarista coriifolia is extremely variable in unicellular indumentum, shape and size of the leaves, development of abaxial laminar glands, and color of the corolla. This variation has led to the description of numerous species and varieties (e.g., *A. neriifolia, A. pohlii, A. bradei,* or the various varieties of *A. laxiflora*) that cannot be maintained when the total pattern of variation is analyzed. Plants with glabrous inflorescence axes and often large leaves lacking abaxial glandular dots along the midvein have often been considered as *A. neriifolia* or *A. coriifolia* sensu stricto, while individuals with pubescent inflorescence axes, and small to large leaves with few to many, conspicuous to inconspicuous abaxial glands along the midvein have been treated as *A. pohlii*. However, these characters are not consistently correlated, and intermediate specimens—e.g., *Harley 15911* (E, L, MO, NY, US), *Harley 18758* (NY), *St.-Hilaire s.n.*, 1816–1821 (P), *St.-Hilaire 234* (P), *Claussen 5* (BM), *Claussen 214* (G), *Barreto 528* (F), *Williams 8130* (GH), and *Pereira 2040* (L)—are common. In addition, both morphological extremes, along with intermediates, grow in the same geographic regions. Thus, these plants are here considered as representatives of a single variable species. Yet specimens previously referred to *A. bradei* (occurring in Minas Gerais, from Diamantina to Chapada in the Serra do Espinhaço) are distinctive due to their leaves that are more or less oblong to slightly elliptic, with cuneate to rounded bases and numerous very conspicuous glandular dots along the midvein abaxially. These populations are here maintained as a weakly delimited variety of *A. coriifolia*. The remaining more variable populations are all treated under var. *coriifolia* due to the lack of any internal discontinuities in the pattern of variation. The two varieties are, at least in part, geographically separate (MAP 5), but both may occur together in the Diamantina region, and the factors isolating them are in need of field investigation.

10. **Agarista pulchra** (Cham. & Schldl.) G. Don, Gen. Syst. **3:** 837. 1834.

Andromeda pulchra Cham. & Schldl. Linnaea **1:** 521. 1826. *Leucothoë pulchra* (Cham. & Schldl.) DC. Prodr. **7:** 604. 1839. *Andromeda sellowii* Steudel, Nomencl. Bot. **2:** 89. 1841, nomen superfl. TYPE: Brazil, without definite locality, *Sellow s.n.* (holotype, B (destroyed); fragment of holotype, NY; isotypes, E!, G!, K!).

Gaylussacia leptobotrys DC. Prodr. **7:** 560. 1839. TYPE: Brazil, Minas Gerais, Serra de Piedade, Nov. 1834, *Lund s.n.* (holotype, G-DC; fragment of holotype, NY; isotypes, C!).

Leucothoë pulchra (Cham. & Schldl.) DC. var. *parvifolia* Meissner *in* Martius, Fl. Brasil. **7:** 161. 1863. TYPE: Brazil, Minas Gerais, without definite locality, 1843, *Claussen 159* (lectotype (selected by Sleumer, 1959), BR; isolectotypes, G!, NY!).

Shrub to ca. 1 m tall. Twigs glabrous to very sparsely pubescent, with nonseptate pith. Buds to ca. 1.3 mm long. Leaves alternate; petiole 1–5 mm long; blade revolute in bud, ovate to elliptic, 1.3–3.5(–4.3) by 0.8–2(–2.5) cm, ± flat, usually very coriaceous, the apex acute- to rounded- or retuse-mucronate, the base cordate to rounded, the margin entire, plane, the adaxial surface glabrous to sparsely pubescent on proximal portion of midvein, the abaxial surface glabrous, usually with few to several inconspicuous to conspicuous glandular dots along midvein. Inflorescences axillary racemes to 4–12 cm long, axis glabrous to very sparsely (moderately) pubescent. Pedicels 3.5–7(–8) mm long, glabrous to sparsely (rarely moderately) pubescent; bracteoles 2, alternate to subopposite, from nearly basal to within lower ⅓ (to near middle) of pedicel, triangular to narrowly so, to ca. 1.2 mm long; bracts to 1.7 mm long. Calyx lobes triangular with acuminate apices, 1.2–2 by 0.6–1.3 mm, abaxial surface glabrous (to rarely sparsely to moderately pubescent); corolla cylindrical, 6–8.5(–9) by 2.5–4 mm, white (to reddish), abaxially glabrous; filaments 3.5–5 mm long, anthers 1.1–1.3 mm long; ovary glabrous (rarely sparsely to moderately pubescent). Capsules subglobose to short-ovoid, 3.5–4.5 by 5–7 mm, placentae subapical (to occasionally ± central); seeds 1–1.5 mm long.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, small region of south-central Minas Gerais (MAP 5). Open campo and slopes, low, dense woodland and thickets; iron-rich soil. Flowering September through January.

REPRESENTATIVE SPECIMENS. **Brazil.** MINAS GERAIS: Camarinhas, Serra do Ouro Prêto, *Barreto 9065* (F); Morro de Santa Anna, Ouro Prêto, *Barreto 9070* (F); Serra da Piedade, *Damazio 1240* (G), *Glaziou 20390* (C, G, K), *Riedel 2666* (G, L, NY); Serra de José d'El Rey and Ouro Prêto, Campo de São Sebastião, *Glaziou 15173* (C); Caeté, Serra da Piedade, *Ianna & Strang 1975/1486* (L); Serra da Piedade, ca. 40 km E of Belo Horizonte, near BR-31, *Irwin et al. 30468* (NY, US); Serra de Ouro Branco, *St.-Hilaire s.n.*, 1816–1821 (NY, P).

Agarista pulchra is apparently closely related to *A. coriifolia* and *A. subrotunda*. It can be distinguished from the former by its usually glabrous (vs. glabrous to densely pubescent) inflorescence axis and its usually smaller, broader leaves with a length/width quotient of 0.9–1.7 (vs. ca. 1.8–6), and from the latter by its glabrous abaxial leaf surface and corolla. The factors isolating these taxa are in need of field study. See illustration in Hooker (1847, *t. 4313*).

Several specimens—for example, *St.-Hilaire s.n.*, 1816–1821—are unusual

because of their rather large leaves and their capsules with central placentae. These plants are tentatively placed here, although they also show similarities to *Agarista coriifolia*.

11. **Agarista subrotunda** (Pohl) G. Don, Gen. Syst. **3:** 837. 1834.

Andromeda subrotunda Pohl, Pl. Brasil. **2:** 32. *t. 121.* 1828/29. *Leucothoë subrotunda* (Pohl) DC. Prodr. **7:** 603. 1839. TYPE: Brazil, Minas Gerais, São João d'El Rey, Oct. 1819, *Pohl s.n.* (not seen).

Andromeda pistrix Cham. Linnaea **8:** 508. 1833. *Agarista pistrix* (Cham.) G. Don, Gen. Syst. **3:** 838. 1834. *Leucothoë pistrix* (Cham.) DC. Prodr. **7:** 604. 1839. *Leucothoë subrotunda* (Pohl) DC. var. *pistrix* (Cham.) Meissner *in* Martius, Fl. Brasil. **7:** 161. 1863. TYPE: Brazil, Minas Gerais, Serra do Lenheiro, *Sellow s.n.* (holotype, B (destroyed); fragment of holotype, NY).

Shrub to ca. 2.5 m tall. Twigs with or without scattered gland-headed hairs, otherwise densely pubescent, with nonseptate pith. Buds to ca. 1.2 mm long. Leaves alternate; petiole 2–4.5 mm long; blade revolute in bud, ovate to elliptic or nearly orbicular, 1–3.5(–4) by 0.7–2.5(–3.7) cm, flat to slightly abaxially curved, very coriaceous, the apex acute- to rounded- or retuse-mucronate, the base cordate, the margin entire (ciliate due to gland-headed hairs), ± plane, the adaxial surface sparsely pubescent on lamina and midvein, often glabrescent, the abaxial surface with or without gland-headed hairs on midvein, otherwise moderately to densely pubescent on lamina and sparsely to densely pubescent on midvein, with few to several inconspicuous to conspicuous glandular dots along midvein (although these often obscured by dense pubescence). Inflorescences axillary racemes to 4–7 cm long, the axis with or without scattered gland-headed hairs, otherwise densely pubescent. Pedicels 5–12.5 mm long, with or without gland-headed hairs, otherwise densely pubescent; bracteoles 2, alternate to subopposite, from nearly basal to near middle of pedicel, narrowly triangular, to ca. 1.3 mm long; bracts to 2 mm long. Calyx lobes triangular to ovate, with acuminate apices, 1.5–2.5 by 1–2 mm, the abaxial surface sometimes with few gland-headed hairs, otherwise densely pubescent; corolla cylindrical, 6.5–9 by 3–4.5 mm, red, abaxially sparsely to densely pubescent; filaments 3.5–4.5 mm long, anthers 1.5–2 mm long; ovary densely pubescent. Capsules short-ovoid, 4–5 by 6–7 mm, placentae subapical; seeds 1.3–2 mm long (probably also larger).

DISTRIBUTION. Brazil, southern Minas Gerais, region surrounding São João d'El Rey (MAP 5). Circa 1065–1675 m alt. Flowering July and August.

REPRESENTATIVE SPECIMENS. **Brazil.** MINAS GERAIS: Serra de Tiradentes, *Barreto 4787* (L); Serra do Lenheiro, *Glaziou 17110* (C, P); São João d'El Rey, *Sellow s.n.* (E, G, K), *Stephan s.n.*, Aug. 1876 (K).

Agarista subrotunda is likely closely allied with *A. pulchra* and *A. coriifolia*. All of these species have thickly coriaceous, at least occasionally conspicuously gland-dotted leaves, and usually subapical placentae. This species is easily separated from both *A. coriifolia* and *A. pulchra* by its conspicuous abaxially pubescent leaves and corollas. *Agarista chapadensis* has similar abaxially pu-

bescent leaves and flowers and may also be closely related; it can be distinguished from *A. subrotunda* by leaf-base shape (cuneate to rounded vs. cordate) and pedicel length. *Agarista paraguayensis, A. mexicana* var. *pinetorum,* and *A. revoluta* var. *velutina* also have abaxially pubescent leaves, but these taxa differ in many other characters and are not closely related to *A. subrotunda. Agarista subrotunda* appears to be geographically separated from all of the above-mentioned species except *A. pulchra* (MAPS 3, 5, and 6). The taxon has been poorly collected and is in need of field investigation.

12. **Agarista chapadensis** (Kinoshita-Gouvêa) Judd, comb. nov.

Leucothoë chapadensis Kinoshita-Gouvêa, Rev. Brasil. Bot. **4**: 127. *fig. 2.* 1981. TYPE: Goiás, Chapada dos Veadeiros, 20 km N of Alto Paraíso, 1600 m alt., 6 March 1983, *Anderson et al. 6502* (holotype, UNB; isotype, NY!).

Shrub or small tree to ca. 3 m tall. Twigs moderately to densely pubescent, with nonseptate pith. Buds to ca. 1 mm long. Leaves alternate; petiole 2–6 mm long; blade revolute in bud, oblong or elliptic to slightly ovate, 2.4–6 by 0.7–2.2 cm, flat, coriaceous, the apex acute- to rounded-mucronate, the base cuneate to rounded, the margin entire, plane, the adaxial surface sparsely pubescent on midvein, the abaxial surface densely pubescent on lamina and midvein (hairs frequently ferrugineous, at least when young) (with few ± inconspicuous glandular dots along midvein, these obscured by dense pubescence). Inflorescences axillary racemes to 4–6 cm long, axis densely pubescent. Pedicels 3–7 mm long, sparsely to densely pubescent; bracteoles 2, alternate to subopposite, from nearly basal to near middle of pedicel, narrowly triangular, to ca. 1 mm long; bracts to ca. 1.3 mm long. Calyx lobes triangular with acuminate apices, 1–2 by 0.7–1.5 mm, abaxial surface moderately to densely pubescent; corolla cylindrical, 6–8 by 3–4.5 mm, white, abaxially moderately to densely pubescent; filaments 4–6 mm long, anthers 1.1–1.4 mm long; ovary densely pubescent. Capsules subglobose to short-ovoid, 4.5–6 by 6–7 mm, placentae subapical; seeds 1.5–3 mm long.

DISTRIBUTION AND ECOLOGY. Central Brazil, Goiás and Bahia (MAP 5). Sandy or rocky campo, rocky (sandstone) open cerrado, moist woods along streams; ca. 1000–1600 m alt. Flowering February and March.

REPRESENTATIVE SPECIMENS. **Brazil.** BAHIA: 4 km N of Rio de Contas, *Mori et al. 12412* (NY). GOIÁS: Chapada dos Veadeiros, ca. 10 km W of Veadeiros, *Irwin et al. 12862* (FLAS, L, NY).

Agarista chapadensis is probably allied with *A. subrotunda*; however, both taxa have been poorly collected and their relationship will remain somewhat obscure until additional material has been collected. The two taxa are distinctive due to their abaxially conspicuously pubescent leaves. Among the South American species of *Agarista,* only *A. paraguayensis* also has similarly pubescent leaves. *Agarista chapadensis* is easily distinguished from *A. subrotunda* by its rounded- to cuneate- (vs. cordate-)based, often longer leaves and by its shorter pedicels; the taxa are geographically separated (MAP 5).

13. **Agarista paraguayensis** (Sleumer) Judd, comb. nov.

Leucothoë paraguayensis Sleumer, Bot. Jahrb. **78:** 465. 1959. TYPE: Paraguay, Paraguarí, Piribebuy, Salto Piravetá, 23 Nov. 1950, *Sparre & Vervoorst 501* (holotype, LIL; isotypes, C!, K!, S!).

Leucothoë paraguayensis Sleumer var. *calva* Sleumer, Bot. Jahrb. **78:** 465. 1959. TYPE: Paraguay, Amambay, Sierra de Amambay, Cerro Corá, Aug. 1933, *Rojas 6189* (holotype, SI).

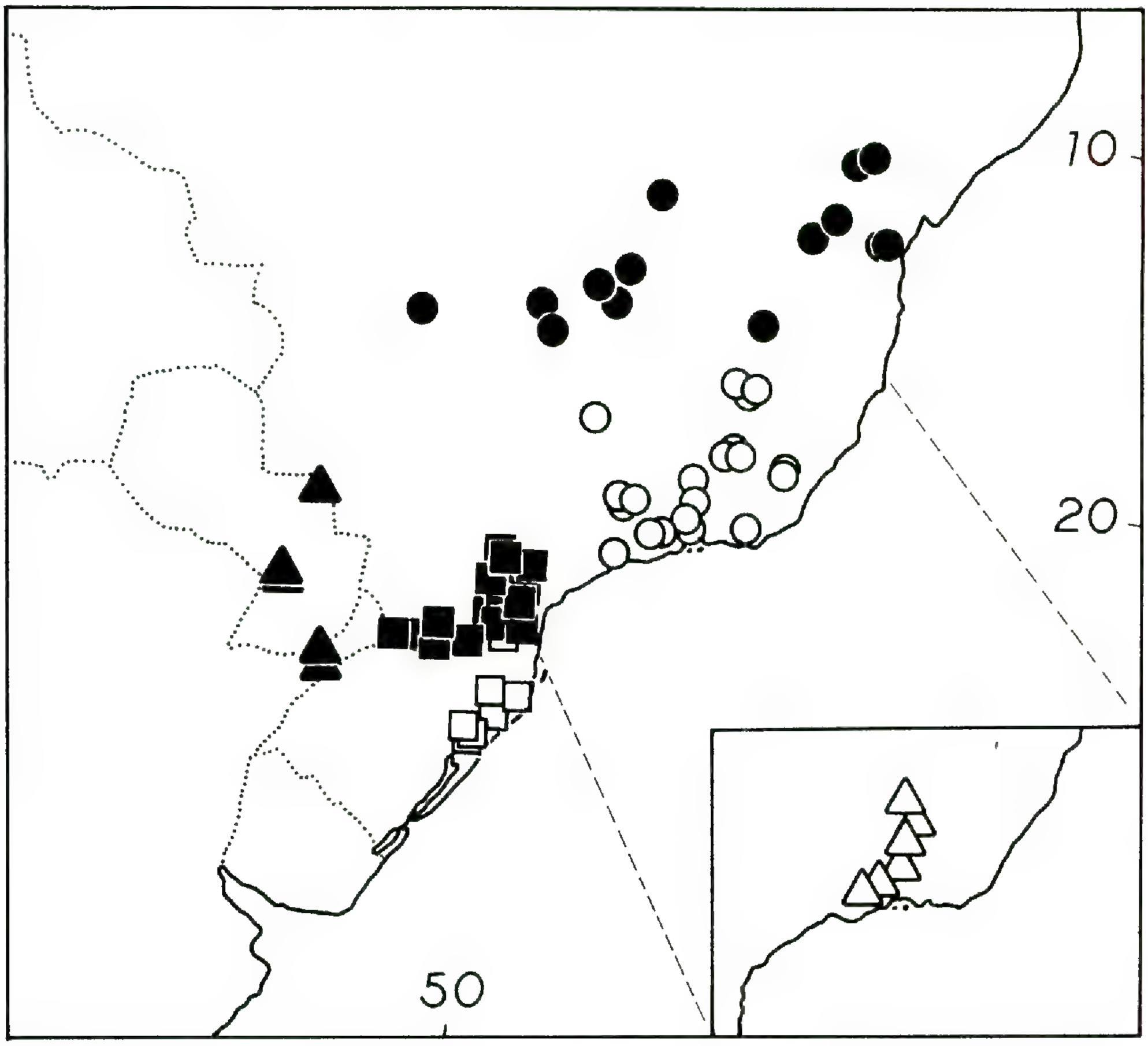
Shrub to ca. 3 m tall. Twigs with or without scattered gland-headed hairs, otherwise sparsely to densely pubescent, with nonchambered to hollow or very sparsely septate pith. Buds to ca. 2.5 mm long. Leaves alternate; petiole 2.5–6 mm long; blade revolute in bud, ovate, 1.8–5.2 by 0.7–2.2 cm, ± flat, coriaceous, the apex acute- to rounded-mucronate or slightly acuminate, the base rounded to cordate, the margin entire (slightly undulate), plane to very slightly revolute, especially near base, the adaxial surface pubescent on midvein (also with few unicellular hairs on lamina), the abaxial surface densely to irregularly and sparsely pubescent on midvein and lamina (glabrous or with pubescence limited to midvein), often with inconspicuous glandular dots along midvein. Inflorescences axillary racemes to 1.5–9 cm long, the axis with or without scattered gland-headed hairs, otherwise moderately to densely pubescent. Pedicels 3–9 mm long, with or without gland-headed hairs, otherwise densely to moderately (sparsely) pubescent; bracteoles 2, opposite to alternate, from nearly basal to within lower ⅓ of pedicel, narrowly triangular, to ca. 1.5 mm long; bracts to 1.5 mm long. Calyx lobes triangular with acuminate apices, 0.9–2.5 by 0.9–1.8 mm, the abaxial surface sometimes with few gland-headed hairs, otherwise sparsely to densely pubescent; corolla cylindrical, 6.5–9 by 3–4 mm, red to white(?), abaxially slightly to very slightly pubescent (to glabrous?); filaments 4.5–5.5 mm long, anthers 1.1–2 mm long; ovary nearly glabrous to densely pubescent. Capsules subglobose, 3.5–4.5 by 5–6.5 mm, placentae ± central; seeds 0.9–1.8 mm long.

DISTRIBUTION AND ECOLOGY. Eastern Paraguay and adjacent Argentina (MAP 6). Rocky areas, steep slopes, ravine slopes along arroyos. Flowering August to December.

REPRESENTATIVE SPECIMENS. **Paraguay:** Campt. Yagin, *Chodat s.n.*, 1914 (G); Cordillera Tobaty, Cerro Tobaty, *Schinini 7920* (L). **Argentina:** Misiones, dept. San Ignacio, Teyucuaré, Peñón Reina Victoria, *Schinini 5499* (F, L, MO); Teyucuaré, *Medan et al. 108* (BAA).

This poorly known species is the only taxon of *Agarista* known to occur in either Paraguay or Argentina. It is probably allied with *A. oleifolia* and *A. pulchella,* from which it can be distinguished by its distinctive combination of often abaxially pubescent leaves and corollas and more or less hollow pith. *Agarista paraguayensis* is superficially similar to *A. mexicana* var. *pinetorum, A. revoluta* var. *velutina, A. chapadensis,* and *A. subrotunda,* all of which have abaxially pubescent leaves. However, it differs from them in placenta position, seed length, and pith structure.

This taxon is variable in leaf indumentum. The leaves of many individuals



MAP 6. Distribution of *Agarista oleifolia* var. *oleifolia* (circles), *A. oleifolia* var. *glabra* (dots), *A. paraguayensis* (solid triangles), *A. minensis* (open squares), *A. pulchella* var. *pulchella* (solid squares), and *A. pulchella* var. *cordifolia* (open triangles).

have a more or less moderate to dense layer of unicellular hairs on the abaxial surface, but those of some plants (e.g., *Sparre & Vervoorst 501*) are essentially glabrous beneath. The taxonomic significance of this variation will remain unknown until the taxon is better known and has been studied in the field.

14. **Agarista oleifolia** (Cham.) G. Don, Gen. Syst. **3:** 838. 1834.

Shrub (to small tree) to 3(–6) m tall, with thickly furrowed bark and often tortuous branches. Twigs with or without scattered gland-headed hairs, otherwise glabrous to sparsely pubescent, with nonchambered to clearly chambered pith. Buds to ca. 1 mm long. Leaves alternate (to nearly 3-whorled); petiole 2–11.5 mm long; blade revolute in bud, (very narrowly) ovate to elliptic or oblong, (2–)2.5–10(–12.5) by 0.4–3.3 cm, ± flat, coriaceous, the apex acute- to rounded-mucronate (slightly acuminate), the base cuneate to rounded or slightly cordate, the margin entire (slightly undulate), plane to very slightly revolute, especially near base, the adaxial surface nearly glabrous to sparsely pubescent on midvein, especially proximal portion, the abaxial surface glabrous to sparsely pubescent

on midvein, usually with inconspicuous glandular dots along midvein. Inflorescences axillary racemes to (2.5–)3–13 cm long, the axis with or without scattered gland-headed hairs, otherwise glabrous to densely pubescent. Pedicels 2.5–15 mm long, with or without gland-headed hairs, otherwise glabrous to densely pubescent; bracteoles 2 (rarely 3), alternate to subopposite, from nearly basal to near midpoint of pedicel (rarely with 1 near apex), to ca. 1.5 mm long; bracts to 2 mm long. Calyx lobes triangular with acuminate apices, 1.4–2.7(–3) by 0.8–2.1 mm, the abaxial surface with or without gland-headed hairs, otherwise glabrous to moderately pubescent; corolla cylindrical, 7.5–16 by (2.5–)3–6.5 mm, red to white, abaxially glabrous; filaments 5.3–8.5 mm long, anthers 1–2.2 mm long; ovary glabrous to sparsely pubescent. Capsules subglobose to short-ovoid, 2.5–5.5 by 4–8 mm, placentae ± central; seeds 0.5–1.3 mm long.

DISTRIBUTION. Southeastern Brazil, from Bahia, Goiás, and extreme southeastern Mato Grosso south to Estado do Rio and São Paulo.

KEY TO THE VARIETIES OF AGARISTA OLEIFOLIA

1. Inflorescence axis sparsely to densely pubescent; corolla 7.5–12 mm long. ..... 14a. var. *oleifolia*.
1. Inflorescence axis glabrous or essentially so; corolla 10.5–16 mm long. ..... 14b. var. *glabra*.

14a. **Agarista oleifolia** (Cham.) G. Don var. **oleifolia** FIGURE 3, b.

Andromeda oleifolia Cham. Linnaea **8:** 504. 1833. *Leucothoë oleifolia* (Cham.) DC. Prodr. **7:** 605. 1839. TYPE: Brazil, Minas Gerais, Itambé, *Sellow s.n.* (holotype, B (destroyed); fragments of holotype, F!, NY; photos of holotype, F, GH!; isotypes, E!, G!, K!, L!).

Leucothoë ambigua Meissner var. *tomentella* Meissner *in* Martius, Fl. Brasil. **7:** 156. 1863 (= *L. ambigua* var. *ambigua*; chosen as nominal variety of *A. ambigua* by Sleumer, 1959, since Meissner described six named varieties of this taxon at the same time). *Agarista ambigua* (Meissner) J. D. Hooker ex Niedenzu, Bot. Jahrb. **11:** 236. 1889. TYPE: Brazil, Minas Gerais, *Martius 837* (lectotype, M! (= holotype of *L. ambigua* var. *tomentella*); fragment of lectotype, F!; isolectotypes, G!, GH!, K!, L!, M!, MO!, NY!, W; photos of isotype, B (destroyed), G!, GH!).

Leucothoë ambigua Meissner var. *hispidula* Meissner *in* Martius, Fl. Brasil. **7:** 156. 1863. *Leucothoë oleifolia* (Cham.) DC. var. *hispidula* (Meissner) Sleumer, Bot. Jahrb. **78:** 476. 1959. TYPE: Brazil, Minas Gerais, Carunhanha R., Sertão do Paranán, *Martius 2000* (holotype, M!).

Leucothoë ambigua Meissner var. *pedunculares* Meissner *in* Martius, Fl. Brasil. **7:** 156. 1863. TYPE: Brazil, Minas Gerais, Serra do Frio, July 1846, *Gardner 4987* (holotype, BM (destroyed?); fragment of holotype, NY!; isotypes, E!, F!, G!, GH!, K!, NY!, P!, S!, US!, W).

Leucothoë stenophylla Loesener, Flora **72:** 77. 1889. *Agarista stenophylla* (Loesener) Niedenzu, Bot. Jahrb. **11:** 236. 1889. TYPE: Brazil, Estado do Rio, Serra dos Orgãos, 21 Jan. 1887, *Glaziou 16232* (holotype, B (destroyed); isotype at B! here designated as lectotype; isolectotypes, C!, F!, K!, P!).

Leucothoë rivularis Sleumer, Notizbl. Bot. Gart. Berlin **12:** 481. 1935. TYPE: Brazil, Minas Gerais, Serra do Itatiaia, 2100 m, 27 Dec. 1895, *Ule 3737* (holotype, B (destroyed); fragment of holotype, F!; photos of holotype, F!, GH!; isotype, HBG!).

Shrub (to small tree) to 3(–6) m tall. Twigs glabrous to sparsely pubescent. Leaves with petiole 2–8 mm long; blade (2–)2.5–8.5(–10.5) by 0.4–2.8 cm, base cuneate, abaxial surface glabrous to sparsely pubescent on midvein. Inflorescences (2.5–)3–12 cm long, axis sparsely to densely pubescent. Pedicels glabrous to densely pubescent. Corolla 7.5–12 mm long, red to white; filaments 5.3–6.8 mm long, anthers 1–1.5 mm long; ovary glabrous to sparsely pubescent. Capsules 2.5–4 by 4–6.5 mm.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, southern and central Minas Gerais and adjacent portions of Estado do Rio and São Paulo (MAP 6). Margins of forests and thickets, frequently along rivers or streams, bogs, open rocky campo; 800–2100 m alt. Flowering chiefly August through October.

REPRESENTATIVE SPECIMENS. **Brazil.** ESTADO DO RIO: Itatiaia, *Brade 21265* (L); Novo Friburgo, *Capell s.n.,* 26 Nov. 1953 (L); Serra do Itatiaia, Retiro, *Dusén 529* (S); Montserrat, *Dusén 2124* (GH, S); Parque Nacional do Itatiaia, margins Rio Campo Belo, *Maas & Martinelli 3162* (NY); Itatiaia, Abrigo Rebouças, *Santos 5755* (L). MINAS GERAIS: Andrelândia, Fazenda da Parahyba, *Barreto 5276* (F, L, NY); Rio Viravinha, *Burchell 5495* (GH, K); Cachoeira do Campo, *Casaretto 2861* (G); Curvello and Rio San Francisco, *Claussen s.n.,* 1837 (L); Fazenda de Manoel José, *Damazio 960* (G); Tiradentes, *Duarte 35505* (F, G, L, S); Rio das Velhas, Itabirito, *Glaziou 15171* (C, G, US); Pico Itambé, S. Antonio do Itambé, *Hatschbach 27511* (C, L, S, UC); Poços de Caldas, Morro do Ferro, *Leoncini & Roppa 206* (L); Caldas, *Regnell II-179* (C, NY, S, US); Uberaba, *Regnell III-835* (C, NY, S, US); near Villa Rica, Itacolumi, *Riedel 408* (G, GOET, K, L); Pico da Bandeira, near Caparaó, *Shepherd et al. 5799* (F, L); Serra de Curimataí, *St.-Hilaire, Cat. B[1], n. 1997* (P); Serra do Caparaó, Macieiras (Grotão), *Strang 220* (L); Serra do Ouro Prêto, *Ule 2619* (HBG); Tejuco [Diamantina], *Vauthier 5* (G, GH, P). SÃO PAULO: Moóca camp, *Brade 5667* (S, SP); rd. from São Bernardo to São Paulo, *Burchell 4054* (K); Butantan, *Gehrt, SP n. 2083* (SP); Cidade Jardim, *Kuhlmann, SP n. 35241* (SP); Campos do Jordão, *Leite 3615* (A, GH); Serra da Bocaina, S of Itatiaia, *Markgraf & Aparicio 10418* (L).

14b. **Agarista oleifolia** (Cham.) G. Don var. **glabra** (Meissner) Judd, comb. nov. FIGURE 5, a, b.

Leucothoë ambigua Meissner var. *glabra* Meissner *in* Martius, Fl. Brasil. **7:** 156. 1863. *Leucothoë oleifolia* (Cham.) DC. var. *glabra* (Meissner) Sleumer, Bot. Jahrb. **78:** 476. 1959. TYPE: Brazil, Bahia, ca. Moritiba, Serra da Jacobina, 1842–1845, *Blanchet 3562* (holotype, W; isotypes, BR, C!, F(specimen and photo)!, G!, GH(specimen and photo)!, K!, MO!, P!).

Leucothoë ambigua Meissner var. *longifolia* Meissner *in* Martius, Fl. Brasil. **7:** 156. 1863. *Leucothoë oleifolia* (Cham.) DC. var. *longifolia* (Meissner) Sleumer, Bot. Jahrb. **78:** 476. 1959. TYPE: Brazil, Goiás, Arrayas, 1841, *Gardner 3876* (holotype, BM; isotypes, E!, F!, G!, K!, NY!, P!, W).

Leucothoë martii Meissner var. *puberula* Meissner *in* Martius, Fl. Brasil. **7:** 155. 1863. TYPE: Brazil, Minas Gerais/Pernambuco, Rio Fermo, *Martius s.n.* (holotype, M!; fragment of holotype, NY; photo of holotype, GH!; isotypes, G!, M!).

Leucothoë martii Meissner var. *glabra* Meissner *in* Martius, *ibid.* 156. TYPE: Brazil, Minas Gerais/Pernambuco, Rio Fermo, *Martius s.n.* (holotype, M!; isotype, M!).

Leucothoë spectabilis Meissner *in* Martius, *ibid.* 159. *Agarista spectabilis* (Meissner) J. D. Hooker ex Niedenzu, Bot. Jahrb. **11:** 236. 1889. TYPE: Brazil, Goiás, banks of S. Bartholomeo, Chapada de S. Marcos, Aug. 1834, *Riedel 2484* (holotype, LE; isotype, NY!).

FIGURE 5. a, b, *Agarista oleifolia* var. *glabra* (*Irwin & Soderstrom 5830*): in b note glabrous inflorescence axis and flowers articulated with pedicels. c, *A. pulchella* var. *pulchella* (*Hatschbach 19703*): note elongate racemes and cordate-based leaves. d, *A. minensis* (*Ule 1840*): note short racemes and round-based leaves. Scale = 2 cm.

Leucothoë varnhageniana Reichardt, Verh. Zool.-Bot. Ges. Wien **33:** 323. 1884. *Agarista varnhageniana* (Reichardt) Niedenzu, Bot. Jahrb. **11:** 236. 1889. TYPE: Brazil, Goiás, Villa Formosa do Imperatriz, *Seguro 68* (holotype, W; fragment of holotype, F!; photos of holotype, A!, F!).

Shrub (to small tree) to 3(–4) m tall. Twigs glabrous. Leaves with petiole 4–11.5 mm long; blade (2.5–)3.5–10(–12.5) by 0.9–3.3 cm, base cuneate to rounded, abaxial surface glabrous. Inflorescences 6–13 cm long, axis glabrous or essentially so. Pedicels glabrous. Corolla 10.5–16 mm long, red (rarely white); filaments 6.5–8.5 mm long, anthers 2–2.2 mm long; ovary glabrous. Capsules 3.5–5.5 by 5.5–8 mm.

DISTRIBUTION AND ECOLOGY. South-central Brazil, from Bahia and northern Minas Gerais east to Goiás and southeastern Mato Grosso (MAP 6). Scrub vegetation over sandstone, woodland and thickets, especially along rivers or streams; ca. 700–1700 m alt. Flowering chiefly August through October.

REPRESENTATIVE SPECIMENS. **Brazil.** BAHIA: Serra do Rio de Contas, 3 km N of town of Rio de Contas, *Harley et al. 15383* (E, L, NY, US); Serra do Sincorá, by Rio Cumbuca, 3 km N of Mucugê on rd. to Andaraí, *Harley 18705* (NY); Serra do Tombador, 18 km E of Morro do Chapéu, Rio Ferro Doido, *Irwin et al. 32626* (FLAS, NY); Lençóis, rd. to Barro Branco, *Mori & Funch 13349* (NY). DISTRITO FEDERAL: Parque Municipal do Gama, ca. 20 km S of Brasília, *Irwin & Soderstrom 5830* (C, F, L, MO, NY, SP, US). GOIÁS: Meia Ponte, near Rio das Almas, *Glaziou 21690* (C, K, P, S); ca. 5 km S of Cristalina, *Irwin et al. 9852* (F, NY); along Rio de Passa Quatro, Joaquim Diaz, *St.-Hilaire, Cat. C, n. 869* (L, P). MATO GROSSO: Rib. Claro, Alto Araguaia, *Hatschbach 35079* (L). MINAS GERAIS: near Grão Mogol, *Williams & Assis 8190* (GH).

Agarista oleifolia is probably most closely related to *A. pulchella, A. minensis,* and *A. paraguayensis.* All four species have moderate to large, flat leaves and capsules with more or less centrally positioned placentae. *Agarista oleifolia* is easily distinguished from *A. paraguayensis* by its abaxially glabrous corollas and leaves and its solid to chambered pith, and from *A. minensis* by its longer inflorescences and often wider leaves. *Agarista oleifolia* is geographically separated from both of these species. It can be distinguished from the very similar but geographically separated *A. pulchella* var. *pulchella* by its differently shaped leaves and its often longer petioles; in addition, the sympatric *A. pulchella* var. *cordifolia* can be readily distinguished by its usually subapical placentae and its smaller leaves. Individuals of *A. oleifolia* are also sometimes confused with *A. uleana, A. niederleinii* var. *acutifolia,* and *A. coriifolia*; see distinguishing characters in key.

Populations of *Agarista oleifolia* are separable into two morphologically distinctive and geographically separate varieties. The more northern, var. *glabra,* is best distinguished from var. *oleifolia* by its glabrous (vs. sparsely to densely covered with short unicellular hairs) inflorescence axis and its usually larger, more frequently red corollas. Variety *oleifolia* has been illustrated by Meissner (1863, *t. 58*).

Both taxa are variable in glandular indumentum and leaf shape, which has led to the description of numerous species and varieties (see synonymy) that cannot be maintained when the entire range of variation is considered. Indi-

viduals with small, very narrowly ovate, acute-apexed leaves are frequent in the Serra do Itatiaia (and also occur in the Serra dos Órgãos). Such plants were described as *Leucothoë stenophylla* by Loesener (1889) and maintained as a distinct species by Sleumer (1959); however, this form intergrades completely with more typical *A. oleifolia* (see *Dusén 2124* (GH, S), *Dusén s.n.*, 15 June 1902 (S), *Dusén s.n.*, 22 July 1902 (S)). Such narrow-leaved plants have occasionally been confused with *A. minensis*.

Several specimens from São Paulo (i.e., *Hoehne, SP no.* (SP), *Lutz 770* (NY, US), *Lutz 1920* (L)) have small, ovate, ± revolute, abaxially curved leaves, and *Lutz 770* has robust capsules with ± subapical placentae. These individuals may be hybrids between *Agarista oleifolia* and a species with small, strongly revolute leaves such as *A. hispidula* or *A. chlorantha*. *Leite 3615* (A, GH) has slightly ferrugineous hairs on its inflorescence axes and may represent a hybrid with the sympatric *A. eucalyptoides*.

15. **Agarista minensis** (Glaz. ex Sleumer) Judd, comb. nov. FIGURE 5, d.

Leucothoë minensis Glaz. Bull. Soc. Bot. France **57:** 129. 1910, nomen nudum. *Leucothoë minensis* Glaz. ex Sleumer, Notizbl. Bot. Gart. Berlin **12:** 480. 1935. TYPE: Brazil, Minas Gerais, Biribiry, Mocotó, near Diamantina, 28 March 1892, *Glaziou 19572* (holotype, B (destroyed); isotype at K! here designated as lectotype; isolectotype, P!).

Shrub to 4 m tall. Twigs glabrous to sparsely pubescent, with clearly chambered pith. Buds to ca. 0.8 mm long. Leaves alternate; petiole 2–6 mm long; blade revolute in bud, slightly and narrowly ovate to narrowly oblong, (1–)1.6–5.6 by 0.3–1(–1.7) cm, ± flat, coriaceous, the apex acute- to rounded-mucronate, the base cuneate to truncate, the margin entire, plane to very slightly revolute, especially near base, the adaxial surface sparsely to very sparsely pubescent on proximal portion of midvein, the abaxial surface glabrous (with few very inconspicuous glandular dots along midvein). Inflorescences (fasciclelike) axillary racemes to 0.5–1.5(–2.5) cm long, axis sparsely to densely pubescent. Pedicels 4–10 mm long, very sparsely to moderately pubescent; bracteoles 2, alternate to subopposite, from nearly basal to near midpoint of pedicel, narrowly triangular to linear, to ca. 1.6 mm long; bracts to 1.2 mm long. Calyx lobes triangular with acuminate (to acute) apices, 1.4–2.6 by 0.8–1.4 mm, abaxial surface glabrous to sparsely pubescent; corolla cylindrical, 6.5–11 by 2.5–4.5 mm, white, abaxially glabrous; filaments 5–5.5 mm long, anthers ca. 1.2 mm long; ovary glabrous to very slightly pubescent near apex. Capsules short-ovoid to subglobose, 3–5 mm by 4.5–7.5 mm, placentae ± central; seeds 1–1.5 mm long.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, Santa Catarina and Rio Grande do Sul (MAP 6). Scrub and forests along streams and rivers; 900–1300 m alt. Flowering November through December (January).

REPRESENTATIVE SPECIMENS. **Brazil.** RIO GRANDE DO SUL: Bom Jesus, Fazenda Bernardo Velho, *Rambo 34939* (MO, S); Cambará, near S. Francisco de Paula, *Rambo 36728* (US); Taimbé, near S. Francisco de Paula, *Rambo 49306* (S); Jaquirana, near S. Francisco de

Paula, *Rambo 51933* (S, US); Passo do Inferno, near Canela, *Rambo 56563* (B). SANTA CATARINA: Bom Jardim, São Joaquim, *Reitz & Klein 7968* (L); Campo Alegre, Pinheiral, Morro Iquererim, *Smith & Klein 7968* (L); 2 km W of Rio Capetinga on rd. to Dionísio Cerqueira, *Smith et al. 9622* (US); Serra Geral, Campos de Capivari, *Ule 1840* (HBG, L).

Although this taxon was included in *Agarista niederleinii* by Sleumer (1959), the two species differ greatly in capsule morphology and inflorescence length and are probably not closely related. *Agarista minensis* is actually closely related to *A. pulchella* var. *pulchella,* from which it is distinguished by its shorter inflorescences and its different leaf shape (length/width quotient (2.5–)3–6 vs. (1.4–)1.6–3(–3.5), base cuneate to truncate vs. cordate). (See Emrich & Rambo, 1949, *fig. 20,* and Marques & Klein, 1975, *pl. 6, fig. 9.*) The ranges of the two taxa overlap only slightly (MAP 6). However, some hybridization may be occurring between them because a few specimens of *A. pulchella* (e.g., *Smith & Klein 8470* (L, US), from Santa Catarina) show some *A. minensis*-like characters. *Agarista minensis* is also allied to *A. oleifolia* and can easily be confused with especially small and narrow-leaved individuals of *A. oleifolia* var. *oleifolia.* The two can be distinguished by the length of the inflorescences and shape of the leaves—especially the apex, which is never narrowly acute in *A. minensis* but is usually so in narrow-leaved variants of *A. oleifolia* var. *oleifolia.*

The provenance of the type (*Glaziou 19572*) is very uncertain. These specimens are identical with *Ule 1840* (HBG, L) and *1841* (see Sleumer, 1959), collected in the state of Santa Catarina. However, *Glaziou 19572* was supposedly collected in Minas Gerais near Diamantina! *Glaziou 19572* is the only collection of *A. minensis* from Minas Gerais, an area separate from the major portion of the species' range, Santa Catarina and Rio Grande do Sul. It is very probable that the specimens represented by *Glaziou 19572* were actually sent to Glaziou by Ule, and that the label information was altered by Glaziou; see discussion in Wurdack (1970).

16. **Agarista pulchella** Cham. ex G. Don, Gen. Hist. **3:** 838. 1834.

Shrub to 2(–3) m tall. Twigs with or without scattered gland-headed hairs, otherwise essentially glabrous to densely pubescent, with nonchambered to irregularly chambered pith. Buds to ca. 1 mm long. Leaves alternate; petiole 1.5–5 mm long; blade revolute in bud, ± ovate, 0.5–4(–5) by 0.4–2(–2.8) cm, ± flat, coriaceous, the apex rounded- to acute-mucronate (short-acuminate), the base cordate (to rarely truncate), the margin entire (to serrulate due to gland-headed hairs) (undulate), plane to very slightly revolute, especially near base, the adaxial surface glabrous to sparsely pubescent on midvein, especially proximal portion, the abaxial surface with or without few gland-headed hairs on midvein, otherwise glabrous to sparsely pubescent (with few very inconspicuous glandular dots) on midvein. Inflorescences axillary racemes (axillary panicles, or terminal racemes or panicles) to (1.5–)2–7(–12) cm long, the axis with or without scattered gland-headed hairs, otherwise glabrous to densely pubescent. Pedicels 4–15 mm long, with or without gland-headed hairs, otherwise glabrous to densely pubescent; bracteoles 2 (to 5), alternate to subopposite, from nearly basal to near midpoint (or rarely apex) of pedicel, narrowly

triangular to linear, to ca. 2.2 mm long, occasionally with 1 or more subtending axillary flowers; bracts to 3 mm long. Calyx lobes triangular with acuminate (to acute) apices, 1.4–2.6 by 0.8–1.5 mm, the abaxial surface with or without gland-headed hairs, otherwise glabrous to densely pubescent; corolla cylindrical, 6.5–13 by 3–5.5 mm, white with reddish apex to red throughout, abaxially glabrous to sparsely pubescent; filaments 4–6.5 mm long, anthers 1.2–1.5 mm long; ovary glabrous to densely pubescent. Capsules short-ovoid to subglobose, 3–5 by 4.5–8 mm, placentae central to subapical; seeds 0.8–1.7 mm long.

DISTRIBUTION. Southeastern Brazil, from Paraná and Santa Catarina, and disjunctly to the north in Minas Gerais and adjacent São Paulo.

KEY TO THE VARIETIES OF AGARISTA PULCHELLA

1. Capsules with placentae usually ± central; leaves with length/width quotient (1.4–)1.6–3(–3.5), margin not (rarely slightly) undulate; [Paraná, Santa Catarina, and adjacent portion of São Paulo]. ..... 16a. var. *pulchella.*
1. Capsules with placentae usually subapical; leaves with length/width quotient 0.8–2, margin often clearly undulate; [Minas Gerais and adjacent northern portion of São Paulo]. ..... 16b. var. *cordifolia.*

16a. **Agarista pulchella** Cham. ex G. Don var. **pulchella** FIGURE 5, C.

Andromeda pulchella Cham. Linnaea **8**: 509. 1833, a later homonym of *Andromeda pulchella* Salisb. Prodr. 289. 1796, nomen superfl. (*A. mariana* L. = *Lyonia mariana* (L.) D. Don cited in synonymy). *Leucothoë pulchella* (Cham. ex G. Don) DC. Prodr. **7**: 604. 1839. TYPE: Brazil, Minas Gerais, Antônio Pereira (see Meissner *in* Martius, 1863; locality very questionable since nearly all collections from Paraná or Santa Catarina), *Sellow 4830* (holotype, B (destroyed); fragments of holotype, F!, NY; photos of holotype, F!, GH!).

Shrub to 2(–3) m tall. Twigs glabrous to densely pubescent. Leaves with petiole 1.5–5 mm long; blade 1.2–4(–5) by 0.4–1.8(–2.8) cm, margin not (rarely slightly) undulate; adaxial and abaxial surfaces glabrous to sparsely pubescent on midvein. Inflorescences axillary racemes (axillary panicles, or terminal racemes or panicles) to 2–7(–12) cm long, axis glabrous to densely pubescent. Corolla 7.5–13 by 3–5 mm; filaments 4.8–6.5 mm long. Capsules 3–4 by 5.5–6 mm, placentae ± central (to rarely subapical); seeds 0.8–1.3 mm long.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, Paraná, Santa Catarina, and adjacent regions of São Paulo (MAP 6). Gallery forests along rivers or streams, bogs, thickets or thicket-margins, sandy or rocky campo; (110–)780–1500 m alt. Flowering (August) September through November (December).

REPRESENTATIVE SPECIMENS. **Brazil.** PARANÁ: Rio dos Papagaios, *Dombrowski 3009 & Kuniyoshi 2489* (L); Palmeira, *Dombrowski 6596* (L); Serrinha, *Dusén 6955* (F, GH, MO, S); Villa Velha, *Dusén 7272* (S); Jaguariaíva, *Jönsson 372*[a] (A, S); Lapa, Rio São Vicente, Serrinha, *Hatschbach (Curial) 518* (L, S); Lapa, Rio Passa Dois, *Hatschbach 5097* (US); Arapoti, Rio das Cinzas, Barra do Perdizes, *Hatschbach 7223* (L); Palmeira, Rod. do Café, *Hatschbach 10158* (B); Pôrto Amazonas, Fazenda São Luís, *Hatschbach 10243* (L); Ponta Grossa, Passo do Pupo, *Hatschbach 17380* (L, UC); Balsa Nova, Barra Rio Papagaios, *Hatschbach 19703* (MO, UC); Estr. do Cerne, Serra das Furnas, Piraí do Sul,

Hatschbach & Guimarães 24761 (K, MO, S, UC, US); Morro da Baliza, Lageadinho, Palmas, *Hatschbach 30747* (C, L, UC, US); Serra da Canha, Cerro Azul, *Hatschbach 32608* (C, L, UC); Rod. dos Mineiros, Almirante Tamandaré, *Hatschbach 37224* (L); Estr. Curitiba to Ponta Grossa, km 38, Serra São Luís do Purunã, *Pabst 5909 & Pereira 6082* (L). SANTA CATARINA: Fazenda Carneiros, Caçador, *Klein 3543* (L); Morro do Iquererim, Campo Alegre, *Reitz & Klein 4766* (L, NY, US); 11 km E of Mafra on rd. to Tinguí, *Smith & Klein 8470* (L, US); Irani, Campo de Irani, *Smith & Klein 13030* (GH, L, MO, UC, US, WIS); Fazenda Campo São Vicente, 24 km W of Campo Erê, *Smith & Klein 13832* (L, NY, US). SÃO PAULO: Itararé, Campos de São Pedro, near Serra de Bom Sucesso, Fazenda Ventania, *Mattos 14108* (SP).

16b. **Agarista pulchella** Cham. ex G. Don var. **cordifolia** (Meissner) Judd, comb. nov.

Leucothoë cordifolia Meissner *in* Martius, Fl. Brasil. **7:** 162. *t. 60, fig. 2.* 1863. *Agarista cordifolia* (Meissner) J. D. Hooker ex Niedenzu, Bot. Jahrb. **11:** 236. 1889. *Leucothoë pulchella* (Cham. ex G. Don) DC. var. *cordifolia* (Meissner) Sleumer, Bot. Jahrb. **78:** 473. 1959. TYPE: Brazil, Minas Gerais, Serra do São João d'El Rey and Serra de São José, June 1824, *Riedel 308* (holotype, LE; isotype, NY!).

Shrub to 1.5 m tall. Twigs moderately to densely pubescent. Leaves with petiole 1.5–3 mm long; blade 0.5–3.5 by 0.4–2 cm, margin often clearly undulate; adaxial and abaxial surfaces ± sparsely pubescent on midvein. Inflorescences axillary racemes to (1.5–)2–5.5 cm long, axis densely pubescent. Corolla 6.5–10 by 3.5–5.5 mm; filaments 4–4.5(?) mm long. Capsules 2.5–5 by 4.5–8 mm, placentae usually subapical; seeds ca. 0.8–1.7 mm long.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, Minas Gerais and adjacent São Paulo (MAP 6). Dry, rocky campo; ca. 1600–1700(?) m alt. Flowering March, June, July, and October through December.

REPRESENTATIVE SPECIMENS. **Brazil.** MINAS GERAIS: Serra de Tiradentes, *Barreto 17476* (NY); São José d'El Rey and Ouro Prêto, *Glaziou 17109* (B, C, NY); Serra do Ibitipoca, *St.-Hilaire, Cat. D, n. 238* (P). SÃO PAULO: Serra da Bocaina, *Brade & Duarte 21179* (L); Serra da Bocaina, Vacca Cahio, *Glaziou 8236* (C, G, P, US); Barreiro Co., Serra da Bocaina, Lageado Farm, *Segadas-Vianna 2800* (L); Silveiras Co., Serra da Bocaina, Jardim Farm, *Segadas-Vianna 3256* (L).

Agarista pulchella is most closely related to *A. minensis* and *A. oleifolia.* It can be distinguished from the former by its longer inflorescences and by the length/width quotient (usually 1.6–3 vs. 3–6) and the bases (cordate vs. cuneate to truncate) of its leaves; from the latter, by its often shorter, more consistently ovate, cordate-based leaves with often shorter petioles. The ranges of *A. pulchella* and *A. minensis* overlap slightly (in northern Santa Catarina), and a few intermediate specimens are known (e.g., *Smith & Klein 8470,* L, US); thus, some hybridization may be occurring. *Agarista oleifolia* is geographically separated from the southern *A. pulchella* var. *pulchella,* but it occurs sympatrically with the northern var. *cordifolia. Agarista pulchella* var. *cordifolia* is easily separable from *A. oleifolia* by the characters given above, as well as by its subapical placentae. Intermediate specimens are apparently unknown. Specimens of *A. pulchella* are occasionally identified as *A. niederleinii, A. subcordata,* or *A. coriifolia*; see distinguishing characters given in key.

Populations of *Agarista pulchella* are divisible into two geographically separate varieties (see illustration of var. *pulchella* in Marques & Klein (1975, *pl. 7*), and of var. *cordifolia* in Meissner (1863, *t. 60, fig. 2*)). Variety *pulchella* has been widely collected in Paraná and Santa Catarina, while var. *cordifolia* seems to be uncommon and limited to a small portion of Minas Gerais and adjacent São Paulo (MAP 6). Sleumer (1959) first recognized the close relationship between these two taxa. Although the capsules of *A. pulchella* var. *pulchella* usually have ± central placentae, plants with subapical placentae (e.g., *Jönsson 224*[a], S)—the typical condition in var. *cordifolia*—are known. *St.-Hilaire, Cat. D, n. 238* is here placed in *A. pulchella* var. *cordifolia*; this specimen is aberrant in having moderately pubescent corollas and capsules with central placentae. However, *A. pulchella* var. *cordifolia* sometimes has slightly pubescent corollas (see *Riedel 308,* NY), and individuals with atypical placenta position occur very occasionally in the southern populations of this species. The unusual placenta position could possibly indicate that this specimen is a hybrid with *A. hispidula,* a species with central placentae and conspicuously pubescent corollas that grows sympatrically with *A. pulchella* in southern Minas Gerais. Field studies are necessary to determine the placement of this unusual specimen conclusively.

Agarista pulchella var. *pulchella* is quite variable in the shape and the length/width quotient of its leaves. At one extreme are plants with short, rather broad, clearly cordate-based leaves, and at the other are those with longer, narrower, and only slightly cordate ones. The former plants are vegetatively rather similar to var. *cordifolia* and have often been identified as such, while the latter are easily confused with *A. minensis.*

17. **Agarista nummularia** (Cham. & Schldl.) G. Don, Gen. Syst. **3:** 837. 1834. FIGURE 6, a, b.

Andromeda nummularia Cham. & Schldl. Linnaea **1:** 520. 1826. *Leucothoë nummularia* (Cham. & Schldl.) DC. Prodr. 7: 603. 1839. TYPE: Brazil, Rio Grande do Sul, Pôrto Alegre (see Meissner *in* Martius, 1863), *Sellow 1229* (holotype, B (destroyed); fragment of holotype, F!; photos of holotype, F!, G!, GH!; isotype, G-DC).

Leucothoë nummularia (Cham. & Schldl.) DC. var. *floccigera* Sleumer, Bot. Jahrb. **78:** 460. 1959. TYPE: Brazil, Rio Grande do Sul, Povo Novo, near Pelotas, 12 Nov. 1901, *Malme 401* (holotype, S!; isotypes, GH!, S!).

Erect shrub or subshrub to 2 m tall, with bark usually not well developed. Twigs with or without scattered gland-headed hairs, otherwise sparsely to densely pubescent, with hollow to irregularly chambered pith. Buds to ca. 1.2 mm long. Leaves alternate; petiole 0.5–2.5 mm long; blade revolute in bud, ovate to elliptic or orbicular, 0.5–1.5(–2.3) by 0.5–1.6(–2) cm, ± flat, coriaceous, the apex obtuse- to retuse-mucronate (rarely short-acuminate), the base cordate to ± truncate (rounded), the margin entire to serrulate due to gland-headed hairs (slightly undulate), plane to very slightly revolute near base, the adaxial surface with or without gland-headed hairs, otherwise sparsely pubescent on proximal portion of midvein, the abaxial surface with or without gland-headed hairs on midvein and blade, otherwise glabrous to sparsely pubescent on proximal portion of midvein (with few very inconspicuous glandular dots along midvein).

FIGURE 6. a, b, *Agarista nummularia:* a, *Rambo 53881*; b, *Rambo 48695*. c, *A. virgata* (*Duarte 8098*): note wandlike, rigidly ascending branches. d, *A. chlorantha* (*Ratter et al. 3384*). Scale = 2 cm.

Inflorescences axillary racemes to 1.5–8 cm long, the axis with or without scattered gland-headed hairs, otherwise densely pubescent. Pedicels 4–11 mm long, with or without gland-headed hairs, otherwise densely pubescent; bracteoles 2, alternate to opposite, from nearly basal to within lower ⅓ of pedicel, narrowly triangular to linear, ovate, or elliptic, to ca. 2.5 mm long; bracts to 3 mm long. Calyx lobes triangular with acuminate to acute apices, (2.1–)2.5–5 by 0.7–1.7(–2.2) cm, the abaxial surface with or without gland-headed hairs, otherwise sparsely to densely pubescent; corolla cylindrical, 7–10.5 by 2.5–5 mm, white, abaxially glabrous; filaments 4.5–5.5 mm long, anthers 1–1.7 mm long; ovary densely pubescent. Capsules short-ovoid to subglobose, 3.5–5 by 5–7 mm, placentae subapical; seeds 1.2–2.3 mm long.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, Santa Catarina and Rio Grande do Sul (MAP 7). Rocky areas, bogs, wet forests, and moist thickets; 10–1650 m alt. Flowering (August) September through December (January).

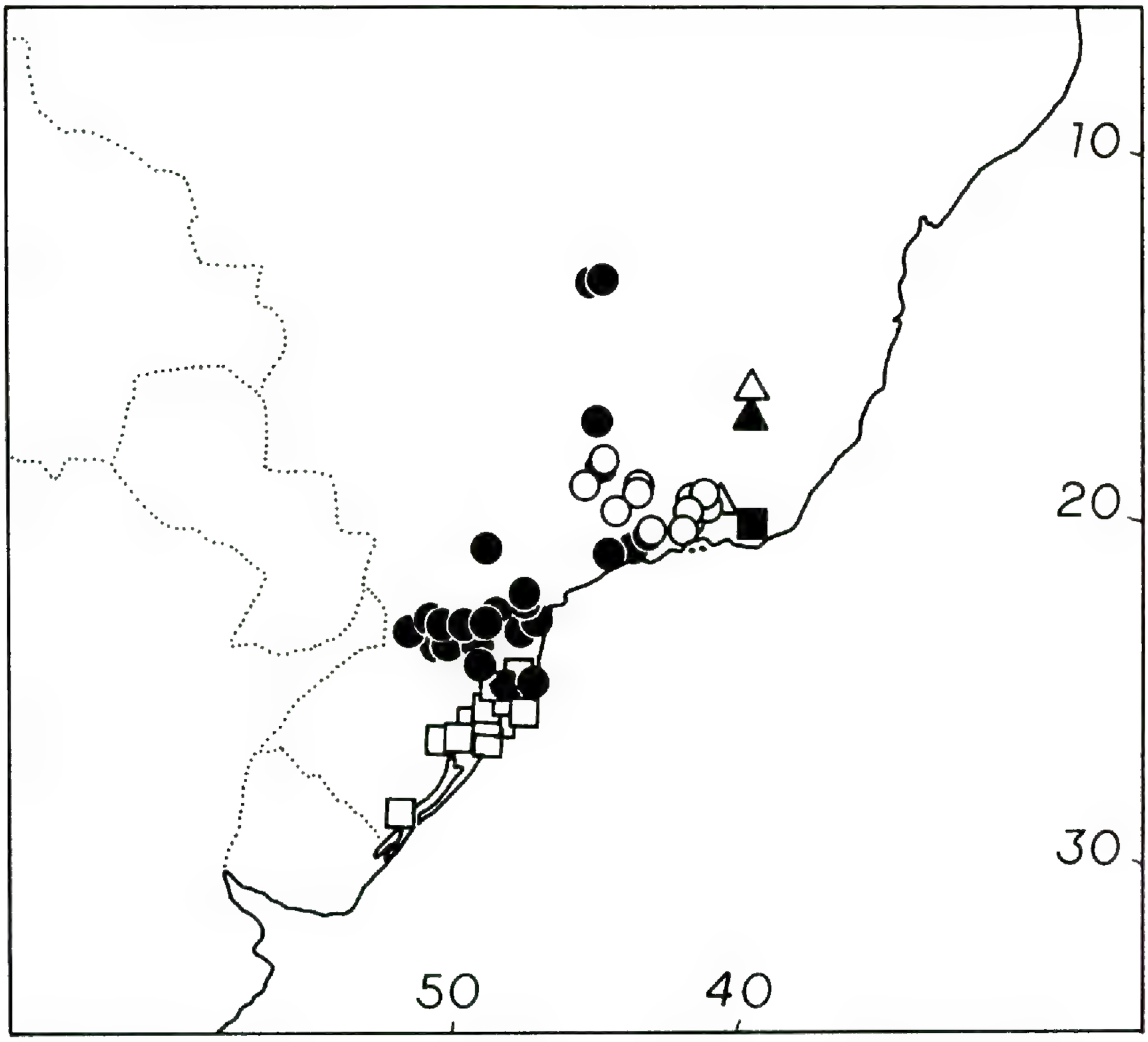
REPRESENTATIVE SPECIMENS. **Brazil.** RIO GRANDE DO SUL: Montenegro, *Camargo 1786* (B); Morro Sapucaia, São Leopoldo, *Leite 3257* (GH); Cachoeira, *Malme 401a* (S); Aparados da Serra, *Pabst 6301 & Pereira 6474* (L); Cambará, S. Francisco de Paula, *Rambo 36724* (B, MO, NY, US); Gravataí, summit Monte Sapucaia, *Rambo 42757* (B, L, US); Sapucaia, São Leopoldo, *Rambo 48695* (B, US); S. Francisco de Paula, *Rambo 52951* (S); Serra da Roçinha, near Bom Jesus, *Rambo 53881* (B); Fazenda Englert, near S. Francisco de Paula, *Rambo 54674* (B); Canela, *Richter 7837* (L). SANTA CATARINA: Serra do Oratório, Bom Jardim, São Joaquim, *Reitz & Klein 7456* (L); Bom Retiro, Fazenda Santo Antônio, Campo dos Padres, *Smith & Reitz 10333* (US); Sombrio, *Reitz 1926* (G, S, US).

Agarista nummularia is probably closely related to *A. chlorantha* and *A. virgata*; it can be separated from the former by its more or less flat, nonrevolute leaves, and from the latter by its sparsely to densely pubescent inflorescence axis, pedicels, and ovaries, and its capsules with more or less subapical placentae. These species are essentially geographically isolated. *Agarista nummularia* may also be confused with small-leaved individuals of *A. pulchella*, a species with shorter calyx lobes that grows to the north of the range of *A. nummularia* (MAPS 6, 7).

The species has been illustrated by Marques and Klein (1975, *pl. 10*).

18. **Agarista virgata** Judd, sp. nov. FIGURE 6, C.

Frutex erectus ad ca. 1 m altus. Ramuli hornotini pilis glandulosis praediti, aliter glabri, cum medulla non septata. Folia ovata vel elliptica, 0.7–1.8 cm longa, 0.7–1.7 cm lata, coriacea, ad apicem brevissime acuminata, acuta vel obtusa cum mucrone brevi, ad basin rotundata vel cordata; margo planiuscula, integra vel minute serrulata; pagina abaxialis pilis glandulosis praedita (praecipue in nervo primario), aliter glabra. Inflorescentiae axillares vel terminales, racemosae vel paniculatae, ad 5–16 cm longae; axis pilis glandulosis praeditus, aliter glaber. Pedicelli 2–7 mm longi, pilis glandulosis praediti, aliter glabri. Flores 5-merus. Calyx lobis 1.4–3 mm longis, 0.6–1.6 mm latis, cum pilis glandulosis in pagina abaxiali. Corolla cylindrica, 6–7 mm longa, 2–3 mm lata, alba, glabra in pagina abaxiali. Filamenta ca. 4 mm longa; antherae ca. 1 mm



MAP 7. Distribution of *Agarista nummularia* (open squares), *A. virgata* (solid triangle), *A. chlorantha* (dots), *A. organensis* (solid square), *A. hispidula* (circles), and *A. ericoides* (open triangles).

longae. Ovarium glabrum. Capsula subglobosa vel brevissime ovoidea, 4–5.5 mm longa, 5.5–7.5 mm lata, cum placentis ± centralibus. Semina 1.2–1.6 mm longa.

Erectly branched shrub to ca. 1 m tall. Twigs with scattered gland-headed hairs, otherwise glabrous, with nonchambered pith. Buds to ca. 2.8 mm long. Leaves alternate; petiole 1–2 mm long; blade revolute in bud, ovate to elliptic, 0.7–1.8 by 0.4–1.3 cm, ± flat, coriaceous, the apex acute- to obtuse-mucronate to short-acuminate, the base cordate to rounded, the margin entire or serrulate due to gland-headed hairs, plane, the adaxial surface with gland-headed hairs, otherwise very sparsely pubescent on extreme proximal portion of midvein, the abaxial surface with gland-headed hairs especially on midvein, otherwise glabrous, usually with few very inconspicuous glandular dots along midvein. Inflorescences axillary racemes or terminal racemes or panicles, to 5–16 cm long, the axis with scattered gland-headed hairs, otherwise glabrous. Pedicels 2–7 mm long, with gland-headed hairs, otherwise glabrous; bracteoles 2, alternate to opposite, from near apex to midpoint of pedicel, narrowly triangular

to ovate, to ca. 2.3 mm long; bracts to 5 mm long (grading into leaves). Calyx lobes triangular with acuminate apices, 1.4–3 by 0.6–1.6 mm, the abaxial surface with gland-headed hairs, otherwise glabrous; corolla cylindrical, 6–7 by 2–3 mm, white, abaxially glabrous; filaments ca. 4 mm long, anthers ca. 1 mm long; ovary glabrous. Capsules subglobose to short-ovoid, 4–5.5 by 5.5–7.5 mm, placentae ± central; seeds 1.2–1.6 mm long.

TYPE. Brazil, Minas Gerais, Serra do Cipó, km 140, 22 June 1964, *A. P. Duarte 8098* (holotype, F!; isotypes, L!, S!).

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, Minas Gerais, Serra do Cipó (MAP 7); ca. 1400 m alt. Flowering in June.

REPRESENTATIVE SPECIMEN. **Brazil.** MINAS GERAIS: Serra do Cipó, km 131, *Duarte 2682* (G, L).

This distinctive species is easily recognized by its rigidly ascending, wandlike branches (from which the specific epithet is derived) with small, more or less flat, densely overlapping leaves. It is most easily confused with the geographically separated *Agarista nummularia* (see MAP 7). However, *A. virgata* is easily separated from *A. nummularia* by its twigs, inflorescence axis, pedicels, and ovaries that completely lack unicellular hairs, and by its capsules with more or less centrally located placentae. This species is also allied with *A. hispidula* and *A. chlorantha.*

It is of interest that both known collections of this taxon have gland-headed hairs; further collecting may reveal plants lacking these hairs, since their presence is variable in all other species in which they occur.

19. **Agarista chlorantha** (Cham.) G. Don, Gen. Syst. **3:** 838. 1934.

FIGURE 6, d.

Andromeda chlorantha Cham. Linnaea **8:** 508. 1833. *Leucothoë chlorantha* (Cham.) DC. Prodr. **7:** 604. 1839. TYPE: Brazil, without definite locality, *Sellow s.n.* (holotype, B (destroyed); fragment of holotype, F!; photos of holotype, F!, G!, GH!; fragment of isotype, NY!).

Amechania subcanescens DC. Prodr. **7:** 579. 1839. *Leucothoë subcanescens* (DC.) Meissner *in* Martius, Fl. Brasil. **7:** 163. *t. 62, fig. 1.* 1863. *Leucothoë chlorantha* (Cham.) DC. var. *subcanescens* (DC.) Sleumer, Bot. Jahrb. **78:** 454. 1959. TYPE: Brazil, São Paulo, Batatais, June 1834, *Lund s.n.* (holotype, G-DC; fragment of holotype, NY; isotype, C!).

Andromeda serrulata Cham. Linnaea **8:** 506. 1833. *Agarista serrulata* (Cham.) G. Don, Gen. Syst. **3:** 838. 1834. *Leucothoë serrulata* (Cham.) DC. Prodr. **7:** 604. 1839. TYPE: Brazil, São Paulo (see Meissner *in* Martius, 1863), *Sellow s.n.* (holotype, B (destroyed); fragments of holotype, F!, NY; photo of holotype, GH!; isotypes, E!, G!, K!).

Erectly branched shrub or subshrub to 1.5 m tall, with bark usually not well developed. Twigs with or without scattered gland-headed hairs, otherwise moderately to densely pubescent, with ± nonchambered to hollow pith. Buds to ca. 0.6 mm long. Leaves alternate; petiole 1–4 mm long; blade revolute in bud, ovate or narrowly ovate to orbicular or even suborbicular, 0.7–2.5 by 0.25–1.3(–1.7) cm, strongly to slightly abaxially curved (rarely ± flat), coriaceous,

the apex acute- to rounded-mucronate, the base cordate, the margin entire, often undulate (serrulate due to gland-headed hairs), strongly to slightly revolute (rarely ± plane), the adaxial surface sparsely pubescent on midvein, especially proximal portion, the abaxial surface with or without gland-headed hairs on midvein, otherwise glabrous to sparsely pubescent on proximal portion of midvein, often with few very inconspicuous glandular dots along midvein. Inflorescences axillary (rarely terminal) racemes to (1–)1.5–8.5 cm long (very rarely flowers solitary, axillary), the axis with or without scattered gland-headed hairs, otherwise moderately to densely pubescent. Pedicels 3.5–13 mm long, with or without gland-headed hairs, otherwise moderately to densely pubescent; bracteoles 2 (rarely several), alternate to subopposite, from nearly basal to within lower ⅓ of pedicel (rarely to near apex), triangular to linear (ovate), to ca. 2.5 mm long; bracts to 3 mm long. Calyx lobes triangular to ovate, with ± acute apices, 2.5–5.5 by 0.8–1.7 mm, the abaxial surface with or without gland-headed hairs, otherwise very sparsely to densely pubescent; corolla cylindrical, 7–11.5 by 3–6.5 mm, white (reddish toward apex), abaxially glabrous; filaments 5.5–6.5 mm long, anthers 1–1.6 mm long; ovary sparsely to densely pubescent. Capsules short-ovoid to subglobose, 3–5 by 4.5–7 mm, placentae subapical; seeds 1–2.1 mm long.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, from Distrito Federal south to Minas Gerais and São Paulo, and disjunctly from Paraná south to Santa Catarina (MAP 7). Wet, boggy or marshy campo, with grasses, sedges, and *Xyris*, open rocky and/or grassy areas, gallery forest; 700–1650 m alt. Flowering late August through December (January).

REPRESENTATIVE SPECIMENS. **Brazil.** DIST. FEDERAL: Córrego Samambaia, near Taguatinga, *Irwin et al. 8151* (NY, SP, UC, US); Rio Torto, N of Brasília, *Irwin et al. 8433* (NY); Fazenda Água Limpa, near Vargem Bonita, 18 km SSW of Brasília TV tower, *Ratter 3050* (E). PARANÁ: Campos do Capão da Imbuia, Curitiba, *Dombrowski 408 & Saito 227* (A, L); Colônia Orleães, Curitiba, *Dombrowski 3088* (L); Pinhaes, *Dusén 7082* (GH, MO, NY, S); Piraquara, Rio Palmital, *Hatschbach 781* (L); Palmas, Sta. Barbara, *Hatschbach 15005* (F, L, NY, UC, US, WIS); Rio Pequeno, S. José dos Pinhais, *Hatschbach 22815* (C, L, UC); S. João do Triunfo, *Hatschbach 17748* (L, UC); Clevelandia, *Hatschbach 22714* (L, UC); S. Jerônimo da Serra, Rio S. Jerônimo, *Hatschbach & Guimarães 24777* (C, S, UC); Rio Atuba, Curitiba, *Hatschbach 32738* (L); Rio Palmital, Colombo, *Hatschbach 32792* (L, MO, UC); União da Vitória, *Koczicki 48* (L, UC); Tatuquara, Curitiba, *Kummrow 692* (L). MINAS GERAIS: Uberaba, *Lund s.n.,* 1843 (C). SANTA CATARINA: Fazenda Carneiros, Caçador, *Klein 3546* (L); Planalto Catarinense, *Pereira 6290 & Pabst 6117* (L); Morro do Iquererim, Campo Alegre, *Reitz & Klein 5220* (L, US); Serra da Boa Vista, São José, *Reitz & Klein 5418* (L, US); Ponte Alta do Norte, Curitibanos, *Reitz & Klein 13386* (L); Valões, *Reitz & Klein 13549* (L); Fazenda Frei Rogério, Pôrto União, *Reitz & Klein 13609* (L); Campo do Areão, Santa Cecília, *Reitz & Klein 14196* (L); Fazenda Ernesto Scheide, Campo Alegre, *Reitz & Klein 5324* (L, US); Bom Retiro, falls of Rio Canoas, Campo dos Padres, *Smith & Klein 7861* (US); Chapecó, Fazenda Campo São Vicente, 24 km W of Campo Erê, *Smith et al. 9525* (L, US); Bom Retiro, Fazenda Santo Antônio, Campo dos Padres, *Smith & Reitz 10331* (L, US); Irani, Campo de Irani, *Smith & Klein 13032* (US); Água Doce, Campos de Palmas, 3 km NW of Herciliópolis, *Smith & Klein 13634* (GH, L, NY, UC, US); 6 km W of Campo Erê, *Smith & Klein 13708* (L, NY, US). SÃO PAULO: Campos do Jordão, *Hashimoto 286* (SP), *Leite 3942* (A, GH); Butantan, *Hoehne,*

SP n. 467 (SP), *572* (SP); Salesópolis, near Rio Coruja, *Mattos, SP n. 157944* (NY); Araramara, *St.-Hilaire, Cat. C*[1] *n. 1004* (P); Urupunga, *St.-Hilaire, Cat. C*[1] *n. 1048* (P).

Agarista chlorantha is most similar to (and easily confused with) *A. hispidula* and *A. organensis*; all three taxa are characterized by more or less erect branches with small, usually ovate, clearly revolute leaves. This species is easily separated from *A. hispidula* by its abaxially glabrous (vs. pubescent) corollas and its more or less acute (vs. acuminate) calyx lobes. It can be distinguished from *A. organensis* by its longer calyx lobes, corollas, and inflorescences, although a few specimens (e.g., *Dombrowski 408, Leite 3942, Mattos, SP n. 157944, Reitz & Klein 5220*) have very short inflorescences or rarely even solitary flowers and thus somewhat approach the latter species. *Agarista chlorantha* is geographically separated from *A. organensis* (see MAP 7), although it grows together with *A. hispidula* in the northern portion of its range (MAP 7). Specimens intermediate between *A. chlorantha* and *A. hispidula* are apparently unknown, but field studies in their area of overlap would be of interest. *Agarista chlorantha* appears to be more common (or at least much better collected) in the southern portion of its range (Paraná and Santa Catarina).

Agarista chlorantha occurs sympatrically with *A. pulchella* over much of its range, and *Hatschbach 17748* (L, UC) may represent a hybrid between these species. This specimen is unusual in its large (to 3.7 by 2 cm) nonrevolute leaves.

Like many other *Agarista* species, *A. chlorantha* is variable in its glandular indumentum. There may be many to few multicellular, gland-headed hairs on the twigs, leaves, inflorescence axis, pedicels, and calyx lobes, or these hairs may be lacking. The plants are alike in all other features, and both indument forms may be found in a single locality (e.g., *Smith & Klein 13634*; *Hoehne, SP n. 467, 572*). Thus, *A. serrulata* and *A. chlorantha,* the former characterized by Sleumer (1959) as being glandular-hairy and the latter as lacking such hairs, are considered to be conspecific. Leaves of *Agarista chlorantha* are also somewhat variable in extent of marginal revolution: those near the base of the plant are frequently less strongly revolute than those toward the distal part of the shoots. In a few plants many of the leaves are only very slightly revolute and more or less orbicular; such plants are easily confused with the closely related *A. nummularia,* a species with consistently plane and widely ovate to elliptic or nearly orbicular leaves.

The species has been illustrated several times—see Meissner (1863, *t. 1, fig. 1*; *t. 62, fig. 1*; *t. 63, fig. 1*) and Marques and Klein (1975, *pl. 9*).

20. **Agarista organensis** (Gardner) J. D. Hooker ex Niedenzu, Bot. Jahrb. **11:** 236. 1889. FIGURE 7, C.

Leucothoë organensis Gardner *in* W. J. Hooker, London Jour. Bot. **4:** 132. 1845. TYPE: Brazil, Estado do Rio, Serra dos Órgãos, ca. 1675 m alt., May 1837, *Gardner 475* (lectotype, K!; isolectotypes, F(fragment)!, G, GH!, NY!, P!; photos of isolectotype, F!, G, GH!).

Erect shrub to ca. 2 m tall. Twigs very sparsely to moderately pubescent, with nonchambered to clearly chambered pith. Buds to ca. 0.7 mm long. Leaves

FIGURE 7. a, b, *Agarista hispidula:* a, *Leite 3477*; b, *Dusen s.n.*, 22 June 1902 (s). c, *A. organensis* (*Glaziou 17119*). d, *A. ericoides* (*Glaziou 19577*). Scale = 2 cm.

alternate; petiole 1.5–4 mm long; blade revolute in bud, ovate (to elliptic), 0.5–1.7 by 0.15–0.8 cm, strongly abaxially curved, coriaceous, the apex acute- to rounded-mucronate, the base cordate to truncate, the margin entire, strongly revolute, the adaxial surface glabrous to sparsely pubescent on midvein, especially proximal portion, the abaxial surface glabrous to sparsely pubescent on midvein, usually with few very inconspicuous glandular dots along midvein. Inflorescences axillary, fasciclelike, often only few flowered racemes to 0.3–1.5 cm long, or flowers solitary and axillary, axis moderately to densely pubescent. Pedicels 4–8 mm long, sparsely to densely pubescent; bracteoles 2 to several, alternate to subopposite, from near base to near midpoint of pedicel, narrowly triangular, to ca. 0.9 mm long; bracts to ca. 1 mm long. Calyx lobes triangular with acuminate apices, 1.1–2 by 0.5–1.2 mm, abaxial surface sparsely to moderately pubescent; corolla cylindrical, 6–7.5 by 2–4 mm, white to red(?), abaxially glabrous; filaments 4–4.5 mm long, anthers 1–1.3 mm long; ovary sparsely to moderately pubescent. Capsules short-ovoid, 3–5 by 4.5–6 mm, placentae subapical; seeds 1–3 mm long.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, Estado do Rio, Serra dos Órgãos (MAP 7). Shrub bogs with *Sphagnum*; ca. 1500–1830 m alt. Flowering November through January.

REPRESENTATIVE SPECIMENS. **Brazil.** ESTADO DO RIO: Serra dos Órgãos, *Gardner 5802* (K, NY), *Glaziou 3763* (C, K, L), *Glaziou 16231* (A, B, C, F, NY, P), *Glaziou 17119* (A, C, F, K, NY, UC, US), *Guillemin 948* (P).

Agarista organensis is very closely related to (and easily confused with) *A. chlorantha*. Both species are shrubs with more or less rigidly ascending branches bearing small, more or less ovate, usually moderately to strongly revolute, cordate-based leaves. *Agarista organensis* can be distinguished from *A. chlorantha* by its short calyx lobes and its very short fasciclelike racemes or its solitary flowers. However, some fasciculate or solitary-flowered variants of *A. chlorantha* are known, and additional collections are necessary in order to clarify the taxonomic value of this character. *Agarista organensis* is geographically isolated; within the genus only *A. oleifolia* also occurs in the Serra dos Órgãos.

21. **Agarista hispidula** (DC.) J. D. Hooker ex Niedenzu, Bot. Jahrb. **11:** 236. 1889. FIGURE 7, a, b.

Amechania hispidula DC. Prodr. **7:** 579. 1839. *Leucothoë hispidula* (DC.) Meissner *in* Martius, Fl. Brasil. **7:** 164. *t. 62, fig. 2.* 1863. TYPE: Brazil, São Paulo, Batatais, June 1834, *Lund s.n.* (holotype, G-DC; fragment of holotype, NY; isotype, C!).

Leucothoë breviflora Meissner *in* Martius, *ibid.* 165. *t. 63, fig. 2. Agarista breviflora* (Meissner) J. D. Hooker ex Niedenzu, Bot. Jahrb. **11:** 236. 1889. TYPE: Brazil, Minas Gerais, Caldas, Oct. 1854, *Lindberg 418* (holotype, BR; fragment of holotype, NY!; isotype, s!).

Leucothoë intermedia Meissner *in* Martius, Fl. Brasil. **7:** 163. *t. 60, fig. 1.* 1863. TYPE: Brazil, Minas Gerais, Caldas, 1845, *Widgren 329* (lectotype (here designated), BR; fragment of lectotype, NY!; possible isolectotype, s!).

Usually erect shrub to 2.5 m tall (but often only ca. 1 m tall), with bark often not well developed. Twigs with or without scattered gland-headed hairs, otherwise sparsely to densely pubescent, with nonchambered to irregularly chambered or sometimes hollow pith. Buds to ca. 0.8 mm long. Leaves alternate; petiole 1–4 mm long; blade revolute in bud, ovate to narrowly ovate, 0.8–2.5(–3.3) by 0.15–1.2 cm, strongly to slightly abaxially curved, coriaceous, the apex acute- to rounded-mucronate (short-acuminate), the base cordate, the margin entire (slightly undulate) (serrulate due to gland-headed hairs), strongly to moderately (only slightly) revolute, the adaxial surface sparsely to densely pubescent on midvein and often with scattered hairs on lamina, the abaxial surface with or without gland-headed hairs on midvein, otherwise sparsely to densely pubescent on midvein and often also sparsely pubescent on lamina (with few very inconspicuous glandular dots along midvein). Inflorescences (very short, fasciclelike) axillary racemes (rarely terminal racemes or panicles) to 0.5–6.5 cm long, axis with or without scattered gland-headed hairs, otherwise densely pubescent. Pedicels 5–13 mm long, with or without gland-headed hairs, otherwise moderately to densely pubescent; bracteoles 2 (rarely 3), alternate to subopposite, from nearly basal to near midpoint of pedicel, narrowly triangular, to ca. 1.8 mm long; bracts to 2.3 mm long. Calyx lobes triangular to ovate with acuminate (to rarely ± acute) apices, 2–5.5 by 0.8–2 mm, abaxial surface with or without gland-headed hairs, otherwise sparsely to densely pubescent; corolla cylindrical to urceolate-cylindrical, 6.5–8.5 by 3–6 mm, red to pink (or white), abaxially sparsely to densely pubescent (rarely also with few gland-headed hairs); filaments 4–5 mm long, anthers 1.4–1.8 mm long; ovary densely pubescent. Capsules short-ovoid, 2.5–5 by 4–7.5 mm, placentae subapical to central; seeds 0.6–1.4 mm long.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, southern Minas Gerais and adjacent São Paulo and Estado do Rio, with one specimen from Goiás (MAP 7). Elfin woodlands, thickets, thicket margins, shrubby grassland, rocky sites, open boggy areas; 1000–2500 m alt. Flowering (June) September through December (February).

REPRESENTATIVE SPECIMENS. **Brazil.** ESTADO DO RIO: Retiro, *Dusén 51* (S); Itatiaia, *Glaziou 8787* (C, L, P); Serra do Itatiaia, W of Retiro de Ramos, *Hemmendorf 586* (S); summit, Mt. Itatiaia, Estação Biologica, *L. B. Smith 1504* (GH, S); Planalto of Itatiaia, 150 km WNW of Rio de Janeiro, *R. & A. Tryon 6696* (NY); Serro do Itatiaia, *Ule 3410* (HBG); Parque Nacional de Itatiaia, *Veloso 304* (NY). GOIÁS: Corumbá, *Glaziou 21621* (P). MINAS GERAIS: Fazenda da Parahyba, Andrelândia, *Barreto 5304* (L); São Thomé das Letras, Baipendi, *Brade 20428* (F, M, US); Pocos de Caldas, *Emmerich 2140* (L); Camanducaia, Vila Monte Verde, *Filho 1869* (L); Caldas, Cervo, *Regnell III-838* (S); Caldas, between Rio Pardo and Corcovado, *Regnell III-839* (P, S); Plateleiras, Agulhas Negras, *Sucre 5767* (F). SÃO PAULO: Campos do Jordão, Reserva do Inst. Forestal, São José dos Alpes, *Davis 3036* (E); São Carlos, *Handro 401* (US); Campos do Jordão, *Kuhlmann 32477* (SP), *Leite 3477* (A, GH, S); Moji-Guaçu, Fazenda Campininha, 3 km NNW of Pádua Sales, *Mattos & Mattos 8214* (K).

Agarista hispidula is most closely related to *A. chlorantha, A. organensis,* and *A. ericoides*; it can be distinguished from all of these species by its abaxially pubescent corollas. In addition, it differs from *A. organensis* in its elongated

calyx lobes, from *A. chlorantha* in its acuminate (vs. acute) calyx lobes, and from *A. ericoides* in its larger leaves.

Sleumer (1959) separated the plants lacking gland-headed hairs as *Leucothoë intermedia,* but these plants are identical in all other characters to the glandular-hairy plants, and both pubescence forms can be found in the same locality (population?) (see *Widgren 329* (BR, S), *Widgren 668* (C, NY, S), *Lindberg 418* (NY, S), *Leoncini & Roppa 341* (L); *Regnell I-186* (F, M, NY, S, US), *Regnell III-838* (S), *Regnell III-839* (S), *Emmerich 2140* (L)).

22. **Agarista ericoides** Taubert, Bot. Jahrb. **17:** 512. 1893. FIGURE 7, d.

Leucothoë ericoides (Taubert) Glaz. Bull. Soc. Bot. France **57**(Mém. 3): 430. 1910. TYPE: Brazil, Minas Gerais, Serra dos Cristais, near Diamantina, 1892, *Glaziou 19577* (holotype, B (destroyed); fragment of holotype, F!; photos of holotype, F!, GH!; isotypes, BR, C!, G!, K!, P!).

Leucothoë lycopodioides Sleumer, Bot. Jahrb. **78:** 450. 1959. TYPE: Brazil, Minas Gerais, Serra de Ibitipoca (43°53′, 21°40′), 11 Aug. 1896, *Schwacke 12360* (holotype, P!; photo of holotype, S!).

Leucothoë acicularis Sleumer, *ibid.* 451. TYPE: Brazil, Minas Gerais, without definite locality, 1816–1821, *St.-Hilaire, Cat. B*[1], *n. 2986* (holotype, P!; isotype, P!).

Erect shrub to ca. 0.5(?) m tall. Twigs with or without scattered gland-headed hairs, otherwise glabrous to densely pubescent, with nonchambered pith. Buds to ca. 0.5 mm long. Leaves alternate; petiole 0.5–1.5 mm long, with or without gland-headed hairs adaxially; blade revolute in bud, narrowly ovate to nearly linear, 0.4–1.2 by 0.1–0.25 cm, strongly abaxially curved, coriaceous, the apex minutely acuminate, the base slightly cordate to truncate, the margin entire (to appearing serrulate/ciliate due to presence of many gland-headed hairs), strongly revolute, the adaxial surface with or without gland-headed hairs on extreme proximal portion of midvein, otherwise glabrous to very sparsely pubescent on proximal portion of midvein, the abaxial surface with or without gland-headed hairs along midvein, otherwise glabrous to very sparsely pubescent on extreme proximal portion of midvein, lacking or with few very inconspicuous glandular dots along midvein. Inflorescences axillary racemes to 1.5–3 cm long, the axis with or without scattered gland-headed hairs, otherwise densely pubescent. Pedicels 3.5–11 mm long, with or without gland-headed hairs, otherwise densely pubescent; bracteoles 2, alternate to opposite, from within lower ¼ to near middle of pedicel, narrowly triangular to ovate, to ca. 3 mm long; bracts ca. 3.5 mm long. Calyx lobes narrowly triangular, with long-acuminate apices, 3–6 by 0.4–0.7 mm, the abaxial surface with or without conspicuous gland-headed hairs, otherwise sparsely to densely pubescent; corolla cylindrical, 8–9.5 by 3.5–4 mm, pink to red, abaxially glabrous; filaments ca. 5.7–6 mm long, anthers ca. 1.5 mm long; ovary densely pubescent. Capsules short-ovoid, 3.5–4.5 by 4–5 mm, placentae ± central; seeds 0.7–1.2 mm long.

DISTRIBUTION. Southeastern Brazil, Minas Gerais (MAP 7).

REPRESENTATIVE SPECIMENS. Known only from type collections.

This distinctive but poorly collected species is immediately recognizable due to its small, extremely revolute leaves. It is probably most closely related to

FIGURE 8. a, *Agarista niederleinii* var. *niederleinii* (*Reitz & Klein 5889*). b, *A. niederleinii* var. *acutifolia* (*Hatschbach & Guimarães 25598*). c, *A. boliviensis* (*Steinbach 8568*): note crisped/undulate leaf margins. d, *A. eucalyptoides* (*Williams & Assis 7503*): note elongate, flexuous petioles. Scale = 2 cm.

three species from which it is geographically separated: *Agarista hispidula, A. organensis,* and *A. chlorantha.*

Like many other species of *Agarista,* this taxon is quite variable in glandular indumentum. Some plants are densely covered with multicellular gland-headed hairs on stems and leaves, while others have only a few of these hairs or none at all. This variation thus cannot be used to delimit species, and *Leucothoë lycopodioides* and *L. acicularis* of Sleumer (1959) are reduced to synonymy under *A. ericoides.*

23. **Agarista niederleinii** (Sleumer) Judd, comb. nov.

Shrub to small tree to 5 m tall with longitudinally furrowed bark. Twigs nearly glabrous to moderately pubescent, with nonchambered to clearly chambered pith. Buds to ca. 1 mm long. Leaves alternate; petiole 1.5–8 mm long; blade revolute in bud, ovate to elliptic or oblong, 0.6–5.7 by 0.3–1.7(–1.9) cm, flat to moderately abaxially curved, coriaceous, the apex acuminate or acute- to retuse-mucronate, the base cuneate to rounded (rarely very slightly cordate), the margin entire, plane to revolute, the adaxial surface glabrous, but sparsely pubescent on midvein, the abaxial surface glabrous (very sparsely pubescent along proximal portion of midvein), usually with few very inconspicuous glandular dots along midvein. Inflorescences axillary racemes to 1–3.5(–4.5) cm long, axis moderately to densely pubescent; bracteoles 2, alternate to opposite, from nearly basal to near midpoint of pedicel, triangular to linear, to ca. 1.5 mm long; bracts to ca. 1.7 mm long. Calyx lobes triangular with acuminate apices, 0.8–2.7 by 0.6–1.8 mm, abaxial surface glabrous to moderately pubescent; corolla cylindrical, 5–8 mm long, 2–4 mm wide, white, abaxially glabrous; filaments 4–5 mm long, anthers 0.9–1.5 mm long; ovary glabrous to sparsely pubescent (with few hairs at apex and around base). Capsules short-ovoid to subglobose, 4.5–7 by 5.5–10 mm, very thick walled, placentae subapical; seeds 1.5–3.2 mm long.

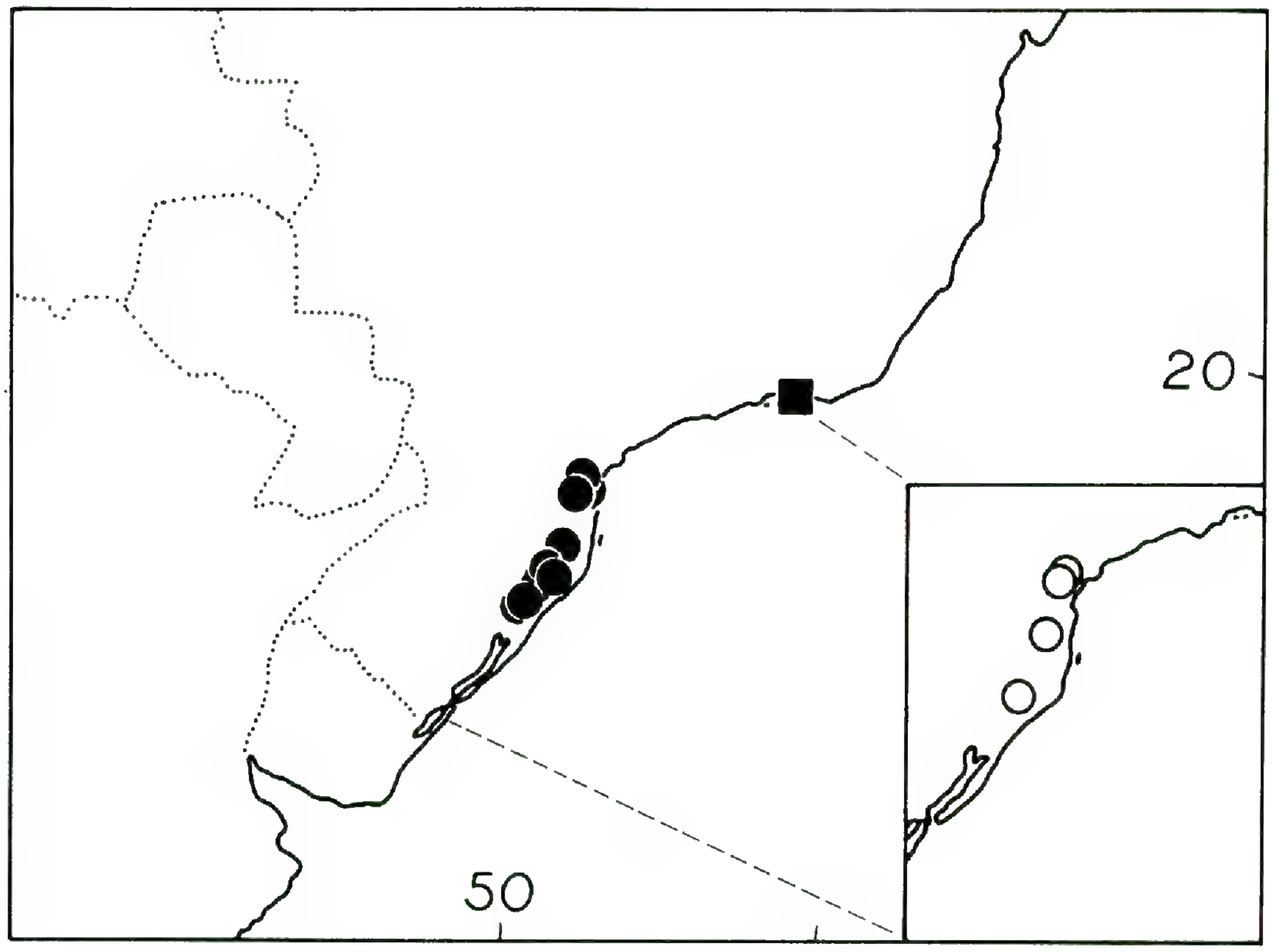
DISTRIBUTION. Southeastern Brazil, from Paraná south to Rio Grande do Sul in the Serra do Mar. Various habitats; 350–2000 m alt.

KEY TO THE VARIETIES OF AGARISTA NIEDERLEINII

1. Leaves with blade 0.6–2.8 by 0.3–0.9 cm, apex usually obtuse- to rounded- or retuse-mucronate; petiole 1.5–4.5 mm long. ..... 23a. var. *niederleinii.*
1. Leaves with blade 2–5.7 by 0.5–1.7(–1.9) cm, apex usually acute-mucronate to acuminate; petiole 3–8 mm long. ..... 23b. var. *acutifolia.*

23a. **Agarista niederleinii** (Sleumer) Judd var. **niederleinii** FIGURE 8, a.

Leucothoë niederleinii Sleumer, Notizbl. Bot. Gart. Berlin **12:** 480. 1935. TYPE: Brazil, Santa Catarina, Campos de los Rios Chopim y Chapecó, Palmas Altas, Jan. 1887, *Niederlein 2006* (holotype, B (destroyed)). The following neotype is here designated: Santa Catarina, Monte Cristo, Garuva, S. Francisco do Sul, *Reitz & Klein 5889* (s!; isoneotypes, B!, L!, NY!, UC!, US!).



MAP 8. Distribution of *Agarista niederleinii* var. *niederleinii* (dots), *A. niederleinii* var. *acutifolia* (circles), and *A. uleana* (square).

Leaves with petiole 1.5–4.5 mm long; blade 0.6–2.8 by 0.3–0.9 cm, flat to moderately abaxially curved, apex usually obtuse- to rounded- or retuse-mucronate, margin plane to revolute. Inflorescences to 1.5–3.5(–4.5) cm long; bracteoles narrowly triangular to linear.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, from Paraná south to Rio Grande do Sul in Serra do Mar (MAP 8). Cloud forests, thickets, and open, rocky crests and slopes; 850–2000 m alt. Flowering November and December (to February).

REPRESENTATIVE SPECIMENS. **Brazil.** PARANÁ: Guaratuba, Serra de Araçatuba, *Hatschbach 6493* (L, UC). RIO GRANDE DO SUL: Taimbesinho, *Araujo 1279* (L); S. Francisco de Paula, Cambará, *Rambo 36724* (NY); Serra da Rocinha, Bom Jesus, *Rambo 53824* (B). SANTA CATARINA: São Joaquim, Serra do Oratório, *Lourteig 2149* (C, P, S, US); Bom Retiro, Campo dos Padres, *Reitz 2338* (B, L, NY, UC, US); Curral Falso, Bom Jardim, São Joaquim, *Reitz & Klein 7794* (L); Morro do Campo Alegre, S. Francisco do Sul, *Reitz & Klein 10322* (L, US); Campo Alegre, Morro Iquererim, *Smith & Klein 8522* (L, US); São Joaquim, Serra do Oratório, 10 km E of Bom Jardim da Serra, *Smith & Reitz 10159* (L, US).

23b. **Agarista niederleinii** (Sleumer) Judd var. **acutifolia** Judd, var. nov.

FIGURE 8, b.

Varietas haec ab Agarista niederleinii var. niederleinii differt in foliis grandioribus 2–5.7 cm longis, 0.5–1.7(–1.9) cm latis, apicibus plerumque acuminatis vel acutatis, mucronibus brevibus, et petiolis longioribus 3–8 mm longis.

Leaves with petiole 3–8 mm long; blade 2–5.7 by 0.5–1.7(–1.9) cm, ± flat, apex usually acuminate to acute- (obtuse-)mucronate, margin plane to very slightly revolute at base. Inflorescences to 1–2.8 cm long; bracteoles triangular.

TYPE. Brazil, Paraná, Campina dos Tavares, Bocaiúva do Sul, 21 Nov. 1970, *G. Hatschbach & O. Guimarães 25598* (holotype, US!; isotypes, C!, M!, MO!, NY!, S!, SP!, UC!).

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, from Paraná south to Rio Grande do Sul in Serra do Mar (MAP 8). Thickets and thicket margins adjacent to grassy campo, stream margins; 350–1000(?) m alt. Flowering November and December.

REPRESENTATIVE SPECIMENS. **Brazil.** PARANÁ: Rio Pequeno, São José dos Pinhais, *Hatschbach 22818* (L, UC, US); Campina dos Tavares, Bocaiúva do Sul, *Hatschbach 23443* (L, NY, US); Guaricana, São José dos Pinhais, *Hatschbach 34903* (NY). RIO GRANDE DO SUL: Taimbesinho, S. Francisco de Paula, *Rambo 54121* (S). SANTA CATARINA: Morro Spitzkopf, *Klein 2318* (L, US), *Reitz 2260* (NY, US); Alto Matador, Rio do Sul, *Reitz & Klein 8303* (L).

Agarista niederleinii is most closely related to *A. uleana,* a geographically isolated species of the Pico da Tijuca region in Guanabara. Both species have distinctive, large, thick-walled capsules with subapical placentae, but they can be distinguished by leaf shape and size, and the extent to which the margins are revolute. The species is also easily confused with *A. minensis* and *A. pulchella,* both of which have smaller, thinner-walled capsules with usually more or less central placentae. In addition, *A. pulchella* has cordate-based leaves and usually longer racemes. It is of interest that Sleumer's (1959) concept of *A. niederleinii* was quite broad, including all of the plants here referred to *A. minensis* and even a few here considered to belong to *A. pulchella.* Although these three species are quite similar in leaf shape and size, they cannot be maintained as a single species because of the great variation in reproductive structures (especially inflorescence and fruit).

Populations of *Agarista niederleinii* are separable into two morphologically distinctive and more or less elevationally isolated varieties. Variety *niederleinii* can usually be separated from var. *acutifolia* by its smaller, usually more or less obtuse-mucronate (vs. acute to acuminate) leaves. Variety *niederleinii,* from the specimens now available, seems to occur at higher and/or more exposed sites than var. *acutifolia,* and it is thus likely that the two taxa are ecologically isolated. However, the two may occasionally grow in close proximity, as they do near Taimbesinho, São Francisco de Paula, and a few more or less intermediate specimens (e.g., *Rambo 54523,* B) are known. These intermediate plants appear to be highly fertile (most pollen grains stain darkly with cotton blue in lactophenol).

Rambo 49305 (S; collected in Taimbe, São Francisco de Paula, Rio Grande do Sul) contains several somewhat aberrant twigs with small, more or less flat, cordate-based leaves. Sleumer (note on sheet) suggested that these plants possibly represent hybrids between *Agarista niederleinii* (var. *niederleinii*) and *A. pulchella* var. *cordifolia* (a taxon with small, cordate-based leaves). However, *A. pulchella* var. *cordifolia* is limited to Minas Gerais and São Paulo and thus

does not occur anywhere near the state of Rio Grande do Sul. These plants are completely fertile (pollen grains stain darkly with cotton blue in lactophenol) and more likely represent merely a cordate-leaved extreme of *A. niederleinii* var. *niederleinii.* Field studies are needed in order to clarify this situation.

24. **Agarista uleana** (Sleumer) Judd, comb. nov.

Leucothoë uleana Sleumer, Notizbl. Bot. Gart. Berlin **12:** 481. 1935. TYPE: Brazil, Guanabara, Rio de Janeiro, Pico da Tijuca, 1000 m alt., Nov. 1897, *Ule 4576* (holotype, B (destroyed); isotype at HBG! here designated as lectotype; isolectotype, R).

Leucothoë ambigua Meissner var. *parvifolia* Meissner *in* Martius, Fl. Brasil. 7: 156. 1863. TYPE: Brazil, Guanabara, Rio de Janeiro, *Riedel s.n.* (holotype, Herb. Sonder; fragment of holotype, NY!).

Shrub to small tree to 3 m tall. Twigs very sparsely to moderately pubescent, with nonchambered to clearly chambered pith. Buds to ca. 1.3 mm long. Leaves alternate; petiole 4–10 mm long; blade revolute in bud, ovate to elliptic (rarely oblong), 2–6 by 0.6–2.1 cm, ± flat, coriaceous, the apex acuminate, to acute with small mucro, the base cuneate to rounded, the margin entire, very slightly revolute (± plane), the adaxial surface glabrous, but sparsely pubescent on proximal portion of midvein, the abaxial surface glabrous (but sparsely pubescent along midvein), usually with few inconspicuous glandular dots along midvein. Inflorescences axillary racemes to 1–2.5(–4) cm long, axis moderately to densely pubescent. Pedicels 3–8 mm long, sparsely to densely pubescent; bracteoles 2, alternate to ± opposite, nearly basal, triangular to narrowly so, to ca. 1 mm long; bracts to ca. 1.5 mm long. Calyx lobes triangular with acuminate apices, 1–2 by 0.6–1.2 mm, abaxial surface glabrous to moderately pubescent; corolla cylindrical, 6.5–10 by 2–4.5 mm, white, abaxially glabrous; filaments 4.5–5.2 mm long, anthers 1–1.6 mm long; ovary glabrous to sparsely pubescent, especially near apex and base. Capsules short-ovoid to subglobose, (3–)4–6 by (5–)5.5–8 mm, very thick walled, placentae subapical; seeds 1.5–2.8 mm long.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, Guanabara, chiefly limited to Pico da Tijuca region (MAP 8). Low forest and scrub, sunny open areas; ca. 700–1020 m alt. Flowering September through November.

REPRESENTATIVE SPECIMENS. **Brazil.** GUANABARA: Pico da Tijuca, *Araujo & Almeida 519* (F), *Duarte 8462* (L, M, NY, S, US); Morro Queimado, *Brade 11108* (GH), *Glaziou 6620* (C, F, NY, P, S); Pedra do Conde, Tijuca, *Lems s.n.,* 22 March 1964 (F, L, M, MO, NY, S). ESTADO DO RIO: see Sleumer (1959).

Agarista uleana is most closely related to *A. niederleinii* and is especially easily confused with *A. niederleinii* var. *acutifolia.* Both species have distinctive, large, thick-walled capsules with subapical placentae. *Agarista uleana* can be separated from *A. niederleinii* var. *niederleinii* by its much larger leaves with acute to acuminate (vs. obtuse- to rounded-mucronate) apices, and from var. *acutifolia* by its slightly different range of leaf shapes and by the extent to which its leaf margins are revolute. The two taxa are geographically separated. Nonfruiting specimens may be confused with *A. oleifolia, A. populifolia,* or *A.*

mexicana, but none of these species occurs in the Pico da Tijuca region; see key for distinguishing characters.

25. **Agarista boliviensis** (Sleumer) Judd, comb. nov. FIGURE 8, c.

Leucothoë boliviensis Sleumer, Notizbl. Bot. Gart. Berlin **12:** 131. 1934. TYPE: Bolivia, Dept. Santa Cruz, valley of Comarapa, 2000 m alt., 26 Oct. 1928, *Steinbach 8568* (holotype, B (destroyed); fragment of holotype, US!; isotypes, BM, E!, F!, G, GH!, K!, LIL, MO!, NY!, S!, UC!; photos of isotype, F!, G, GH!).

Shrub or small tree to ca. 5 m tall. Twigs glabrous, with obscurely chambered pith. Buds to ca. 1 mm long. Leaves alternate; petiole (5–)8–17 mm long, frequently slender and flexuous; blade revolute in bud, ovate, 2–5.5 by 0.9–2.2 cm, ± flat, coriaceous, the apex acuminate, the base rounded and often slightly asymmetric, the margin entire and minutely undulate, ± plane, the adaxial surface glabrous, but usually very sparsely pubescent on midvein, the abaxial surface glabrous, but usually very sparsely pubescent along midvein, with or without inconspicuous to conspicuous glandular dots along midvein. Inflorescences axillary racemes to 1–2.5 cm long, axis moderately pubescent with ± whitish hairs. Pedicels 4–8 mm long, sparsely to moderately pubescent; bracteoles 2, opposite to alternate, from basal to within lower ⅓ of pedicel, narrowly triangular to linear, to ca. 1.1 mm long; bracts to ca. 1.4 mm long. Calyx lobes triangular with acuminate apices, 0.9–1.7 by 0.5–1.5 mm, abaxial surface glabrous to moderately pubescent; corolla cylindrical, 6–9.5 by 3–5 mm, white, abaxially glabrous; filaments 3.5–4.5 mm long, anthers 1–1.1 mm long, ovary glabrous to sparsely pubescent near apex. Capsules subglobose to ovoid, 3.5–4.5 by 5–6.5 mm, placentae subapical; seeds 2–2.5 mm long.

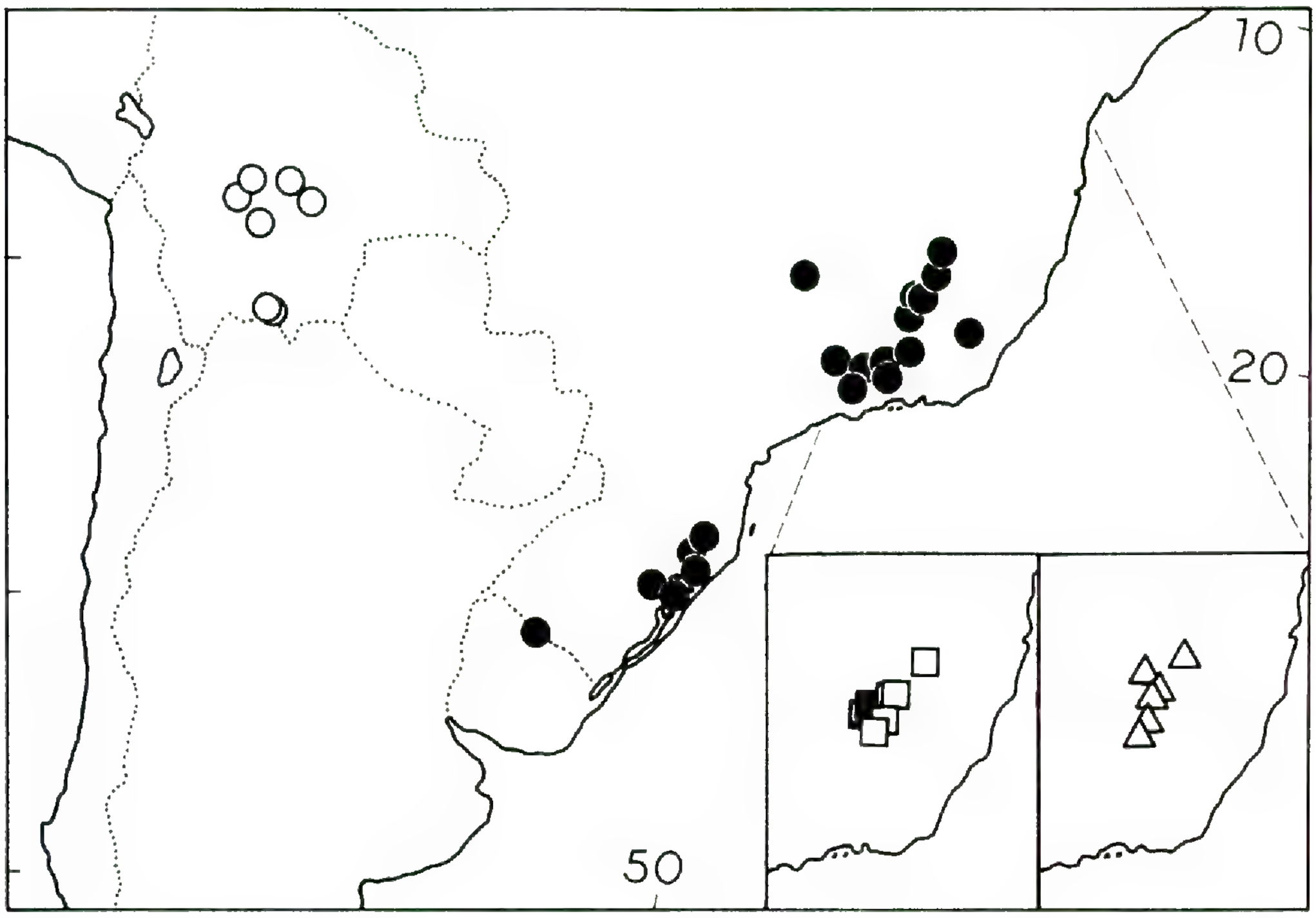
DISTRIBUTION AND ECOLOGY. Bolivia (MAP 9). Mountainous areas ca. 1200–2500 m alt. Flowering September and October.

REPRESENTATIVE SPECIMENS. **Bolivia:** Charcas, San Pedro, Pasopaya, *Anonymous 3400* (GH); Cochabamba, Rosal, below pumping station, *Brooke 5702* (F, NY); Santa Cruz, Tres Cruces, *Herzog 1634a* (L); Sucre, Alto de Aguas Blancas, *Troll 1249* (B); Tarija, Lomas peladas, Alto de las Cañas, *Troll 359* (B, M); Camino de Emborozú, La Mamora, *Türpe et al. 4777* (BAA).

Agarista boliviensis is most closely related to *A. eucalyptoides,* from which it is easily distinguished by its more consistently ovate leaves and its inflorescence axis with whitish (vs. ferrugineous) hairs. Both taxa are distinctive due to their moderate-sized leaves with often elongate and flexuous petioles. *Agarista boliviensis* has consistently crisped/undulate leaf margins, whereas in *A. eucalyptoides* this character is variable. The two species are completely allopatric since *A. eucalyptoides* is limited to southeastern Brazil and Uruguay.

26. **Agarista eucalyptoides** (Cham. & Schldl.) G. Don, Gen. Syst. **3:** 837. 1834. FIGURE 8, d.

Andromeda lanceolata Vell. Conc. Fl. Flum. 175. 1825, later homonym of *A. lanceolata* Wallich, Asiatic Res. **12:** 391. 1820 = *Lyonia ovalifolia* (Wallich) Drude. TYPE: "Cabinet d'Histoire naturelle de Rio de Janeiro" (not seen).



MAP 9. Distribution of *Agarista boliviensis* (circles), *A. eucalyptoides* (dots), *A. glaberrima* (triangles), *A. angustissima* (open squares), and *A. duartei* (closed squares).

Andromeda eucalyptoides Cham. & Schldl. Linnaea **1:** 518. 1826. *Leucothoë eucalyptoides* (Cham. & Schldl.) DC. Prodr. 7: 605. 1839. *Leucothoë multiflora* (Pohl) DC. var. *eucalyptoides* (Cham. & Schldl.) Meissner *in* Martius, Fl. Brasil. 7: 155. 1863. TYPE: Brazil, Rio Grande do Sul, *Sellow s.n.* (holotype, B (destroyed); fragment of holotype, NY; isotypes, BR, E!, G!, K!).

Andromeda multiflora Pohl, Pl. Brasil. **2:** 33. *t. 122.* 1828/29. *Agarista multiflora* (Pohl) G. Don, Gen. Syst. **3:** 837. 1834. *Leucothoë multiflora* (Pohl) DC. Prodr. 7: 605. 1839. *Leucothoë multiflora* (Pohl) DC. var. *pohlii* Meissner *in* Martius, Fl. Brasil. 7: 155. 1863, nomen superfl. TYPE: Brazil, Minas Gerais, Rancho Novo, Serra da Mantiqueira, Sept./Oct. 1819, *Pohl s.n.* (holotype, W (destroyed?); isotypes, BR, M!).

Andromeda longepetiolata Fenzl ex Ettingsh. Blatt-Skel. Dikot. 94. *fig. 56.* 1861. TYPE: not seen.

Leucothoë multiflora (Pohl) DC. var. *petiolaris* Meissner *in* Martius, Fl. Brasil. 7: 155. 1863. TYPE: Brazil, Minas Gerais, Serra de Cural d'El Rey, ca. 1841–1842, *Gardner 4986* (holotype, BM; isotypes, E!, F!, G!, GH!, K!, NY!, P!, US!, W).

Leucothoë multiflora (Pohl) DC. var. *brevipes* Meissner *in* Martius, *ibid.* TYPE: Brazil, Minas Gerais, Tejuco (= Diamantina), *Martius 1337* (holotype, M!; isotype, M!).

Shrub or small tree to ca. 4(–8) m tall, with often contorted trunks and thick, corky, furrowed bark. Twigs glabrous to sparsely pubescent, with ± nonchambered pith. Buds to ca. 1.5 mm long. Leaves alternate to subopposite or ± whorled, often variable even within single twig; petiole 6–40 mm long, frequently slender and flexuous; blade revolute in bud, ovate to oblong, 2.5–8 (–9.3) by 0.8–2.6 cm, ± flat, coriaceous, the apex acute to acuminate or shortly

so, to nearly rounded-mucronate, the base rounded to truncate and often slightly asymmetric, the margin entire (undulate), plane to very slightly revolute, especially near base, the adaxial surface glabrous (sparsely pubescent on midvein), the abaxial surface glabrous (very sparsely pubescent on midvein near base), with usually at least few inconspicuous (to conspicuous) glandular dots along midvein. Inflorescences axillary racemes to 1–6 cm long, axis moderately to densely ferrugineous/crisped-pubescent. Pedicels 2–6 mm long, sparsely to densely ferrugineous-pubescent; bracteoles 2, opposite to alternate, from nearly basal to near midpoint of pedicel, narrowly triangular, to ca. 1.1 mm long; bracts to ca. 1.7 mm long. Calyx lobes triangular with acuminate (to acute) apices, 1–1.8 by 0.5–1.2 mm, abaxial surface essentially glabrous; corolla cylindrical, 6–10.5 by 2.5–5 mm, white (to reddish), abaxially glabrous; filaments 3–4.5 mm long, anthers 0.8–1.1 mm long; ovary glabrous to sparsely pubescent. Capsules ovoid to short-ovoid, 3–5 by 4–5 mm, placentae subapical; seeds 1.8–2.5 mm long.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil (Minas Gerais and adjacent regions of Estado do Rio and São Paulo; Santa Catarina, Rio Grande do Sul) and Uruguay (MAP 9). Cerrado vegetation, open, rocky thickets and thicket margins, or rocky hillsides; (250–)800–2300 m alt. Flowering chiefly late August through November (December).

REPRESENTATIVE SPECIMENS. **Brazil.** ESTADO DO RIO: Nova Friburgo to Pedra do Cônego, *Glaziou 12927* (C, P). MINAS GERAIS: Itatiaia, *Brade 14086* (F, L); Serra do Caparaó, *Brade 16987* (F, L); São Thomé das Letras, Baipendí, *Brade 20429* (F, M); Serra do Cipó, km 131, *Duarte 2693* (F, L); Serra da Moeda, *Duarte 8897* (L, M); Serra do Itatiaia, *Dusén 2011* (G, GH, S); Serra da Mutuca, Belo Horizonte, *Markgraf 3523* (F); 35 km from Lambari, *Pereira 7153* (B); Uberava, *Regnell III-837* (S, US); Pico da Bandeira, near Caparaó, *Shepherd et al. 5795* (L); Caldas, *Widgren 327* (S); Serra da Calveira, Betim, *Williams & Assis 7503* (F, GH, MO, NY, S, SP, US). RIO GRANDE DO SUL: Pôrto Alegre, Morro da Policia, *Malme 608* (S); São Leopoldo, *Rambo 132* (S, SP); Montenegro, Zimmerberg, *Rambo 8309* (B); S. Francisco de Paula, Vila Oliva, *Rambo 31063* (F, MO, S); Pôrto Alegre, Morro da Glória, *Rambo 40072* (B, MO); Passo do Socorro, Vacaria, *Rambo 51626* (S, US). SANTA CATARINA: 16 km E of Lajes on rd. to Painel, *Smith & Reitz 10103* (L, US). SÃO PAULO: Campos do Jordão, *Leite 3614* (A, GH). **Uruguay:** Rivera, Cuñapirú, *Berro 4973* (G); Rivera, Galgo, *Herter 1859* (B, F, G, L, M, MO, NY, S).

Agarista eucalyptoides is a distinctive species easily recognizable by the moderately to densely ferrugineous/crisped pubescence of its inflorescence axis and pedicels. It is most closely related to *A. boliviensis,* a geographically separated species with more consistently ovate leaves and an inflorescence axis with whitish hairs. Both of these species (along with *A. glaberrima* and—to a lesser extent—*A. angustissima*) frequently have slender, flexuous, elongate petioles. Sleumer (1959) considered *A. glaberrima* to be only varietally distinct from *A. eucalyptoides,* but the two taxa differ in leaf shape, degree of adaxial folding of the lamina, inflorescence indumentum (lacking in *A. glaberrima*), and—to a lesser extent—capsule size. The morphological gap separating these taxa is thus comparable to that between most *Agarista* species. *Agarista glaberrima* is considered here to be a distinct species that is probably more closely related to *A. angustissima* than it is to *A. eucalyptoides.*

FIGURE 9. a, *Agarista glaberrima* (*Hatschbach, Smith, & Ayensu 28814*). b, *A. angustissima* (*Hatschbach 27988*, UC): note terminal racemes. Scale = 2 cm.

27. **Agarista glaberrima** (Sleumer) Judd, comb. et stat. nov. FIGURE 9, a.

Leucothoë eucalyptoides (Cham. & Schldl.) DC. var. *glaberrima* Sleumer, Bot. Jahrb. **78:** 458. 1959. TYPE: Brazil, Minas Gerais, Santa Lúcia, Serra do Cipó, km 135, 4 Feb. 1938, *Barreto 8921* (holotype, F!; photo of holotype, F!).

Shrub or small tree to 4 m tall. Twigs glabrous, with nonchambered to clearly chambered pith. Buds to ca. 1 mm long. Leaves alternate; petiole 10–32 mm long, frequently slender and flexuous; blade revolute to conduplicate(?) in bud, ovate to narrowly ovate, 2.3–8.5 by 0.6–2.5(–3) cm, flat to strongly adaxially folded, coriaceous, the apex acuminate, the base cuneate to rounded and often slightly asymmetric, the margin entire (slightly undulate), plane, the adaxial surface glabrous (very sparsely pubescent on proximal portion of midvein), the abaxial surface glabrous, with few to many inconspicuous to conspicuous glandular dots along midvein. Inflorescences axillary racemes, or terminal racemes or panicles, to 1–9.5 cm long, axis glabrous. Pedicels 2.5–8 mm long, glabrous; bracteoles 2, opposite to alternate, from nearly basal to near midpoint of pedicel, narrowly triangular, to ca. 0.9 mm long; bracts to ca. 1.4 mm long. Calyx lobes triangular with acuminate (to nearly acute) apices, 0.8–1.7 by 0.5–1.3 mm, abaxial surface glabrous; corolla ± cylindrical, 6–10 by 2.7–4.5 mm, white or greenish white, abaxially glabrous; filaments 3.5–4.5 mm long, anthers 1.1–1.3 mm long; ovary glabrous or nearly so. Capsules subglobose to short-ovoid, 4–8 by 6–8 mm, placentae subapical to nearly central; seeds 2–2.5 mm long.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, Minas Gerais (MAP 9). Sandy to rocky cerrado vegetation, margins of woods, rocky and/or disturbed thickets, rocky hillsides; 900–1500 m alt. Flowering chiefly November through February.

REPRESENTATIVE SPECIMENS. **Brazil.** MINAS GERAIS: Serra do Espinhaço, Gouvêa, km 258 on M. G. 259, *Anderson et al. 35627* (F, L, NY); Serra dos Cristais, Diamantina, *Barreto 9562* (F); Boa Vista–Extracção, Diamantina, *Barreto 9647* (F); Serra do Cabral, Joaquim Felício, *Davis et al. 2374* (E); Diamantina, *Duarte 10526* (L); Serra do Cipó, Jaboticatuba, *Hatschbach et al. 28814* (C, L, MO, NY, S, UC); Serra do Espinhaço, Lapinha, 19 km N of Cêrro on road to Diamantina, *Irwin et al. 20802* (NY); 12 km NE of Diamantina on rd. to Mendanha, *Irwin et al. 22758* (ENCB, F, GH, K, NY); Serra Grão Mogul, *Maguire et al. 49269* (NY); Serra Negra, *St.-Hilaire, Cat. D, n. 94* (L, P).

Agarista glaberrima is most closely related to the sympatric *A. angustissima,* another Minas Gerais endemic (MAP 9) from which it can easily be distinguished by its ovate and wider leaves with usually longer petioles and less strongly adaxially folded blades. Although Sleumer (1959) considered this species to be a variety of *A. eucalyptoides,* the two taxa are quite distinct and can be separated by inflorescence indumentum (lacking vs. moderate to dense and ferrugineous), leaf shape (ovate vs. ovate to oblong), and degree of adaxial folding of the lamina.

28. **Agarista angustissima** Taubert, Bot. Jahrb. **17:** 513. 1893. FIGURE 9, b.

Leucothoë angustissima (Taubert) Sleumer, Bot. Jahrb. **78:** 451. 1959. TYPE: Brazil, Minas Gerais, Pinheiro, near Biribiri, 26 March 1892, *Glaziou 19582* (holotype, B (destroyed); fragment and photo of holotype, F!; photo of holotype, GH!; isotypes, BR, F!, G!, K!, MO!, NY!, P!).

Shrub to ca. 2 m tall. Twigs with or without gland-headed hairs, otherwise glabrous, with nonchambered pith. Buds to ca. 1 mm long. Leaves alternate; petiole 5.5–13 mm long, often slender and flexuous; blade conduplicate in bud, linear and curved, to narrowly ovate in juvenile leaves, (1.7–)3–7 by 0.1–0.5 cm but often appearing narrower, strongly adaxially folded and thus obscuring adaxial surface, coriaceous, the apex narrowly acute to short-acuminate, the base narrowly cuneate, the margin entire, to serrulate in juvenile leaves due to presence of gland-headed hairs, plane, the adaxial surface glabrous, the abaxial surface with or without gland-headed hairs, otherwise glabrous, lacking or with few inconspicuous glandular dots along midvein. Inflorescences axillary racemes, or terminal racemes or panicles, to 3–6 cm long, axis glabrous. Pedicels 4.5–14 mm long, glabrous; bracteoles 2, alternate to opposite, from nearly basal to within lower ¼ of pedicel, narrowly triangular to linear, to ca. 1 mm long; bracts to ca. 3 mm long, grading into leaves. Calyx lobes triangular with acuminate apices, 1–1.5 by 0.5–1.1 mm, abaxial surface glabrous; corolla cylindrical, 6.5–10.5 by 2.5–3.5 mm, white, abaxially glabrous; filaments 4–5 mm long, anthers 1–1.7 mm long; ovary glabrous. Capsules short-ovoid to subglobose, 3.5–5.5 by 5–7 mm, placentae subapical to nearly central; seeds 1.5–2.9 mm long.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, Minas Gerais (MAP 9). Cerrado vegetation, moist rocky areas; ca. 1200–1400 m alt. Flowering November.

REPRESENTATIVE SPECIMENS. **Brazil.** MINAS GERAIS: Diamantina, *Barreto 10132* (F); Biribiri, Diamantina, *Hatschbach & Pelanda 27988* (C, L, NY, S, UC); Serra do Cipó, Fazenda Palacio, Jaboticatuba, *Hatschbach & Ahumada 31564* (L); Chapada, *St.-Hilaire, Cat. B*[1], *n. 2057* (L, P).

Agarista angustissima is a very distinctive species recognizable by its very narrow, more or less linear/curved leaves that are strongly adaxially folded and ca. 3–7 cm long, its glabrous stems, and its often terminal inflorescences. Most closely related to *A. glaberrima* and *A. duartei,* it can be distinguished from the former by its narrower, linear leaves, and from the latter by its glabrous stems and its more elongated, terminal inflorescences. All three species are limited to the Serra do Espinhaço region of Minas Gerais.

29. **Agarista duartei** (Sleumer) Judd, comb. nov.

Leucothoë duartei Sleumer, Bot. Jahrb. **78:** 451. 1959. TYPE: Brazil, Minas Gerais, Serra do Cipó, km 137 da Estrada de Conceição, 1300 m alt., 6 Dec. 1949, *Duarte 2103* (holotype, RB; isotypes, L!, LIL).

Subshrub to ca. 0.5 m tall, with bark not well developed. Twigs ± glabrous to densely pubescent, with nonchambered to irregularly chambered pith. Buds to ca. 1 mm long. Leaves alternate; petiole 2–6.5 mm long, not flexuous; blade conduplicate in bud, linear and ± curved, 1.2–3.5(–4) by 0.2–0.4 cm but often appearing narrower, strongly adaxially folded and thus obscuring adaxial surface, coriaceous, the apex narrowly acute to short-acuminate, the base narrowly cuneate, the margin entire, to serrulate in juvenile leaves due to presence of gland-headed hairs, plane, the adaxial surface sparsely pubescent, the abaxial surface with or without gland-headed hairs, otherwise glabrous to very sparsely pubescent on proximal portion of midvein, lacking or with few inconspicuous glandular dots along midvein. Inflorescences axillary racemes to 0.3–1.5 cm long, axis very slightly to densely pubescent. Pedicels 2–7.5 mm long, glabrous to densely pubescent; bracteoles 2, subopposite to alternate, from nearly basal to near midpoint of pedicel, narrowly triangular, to ca. 1 mm long; bracts to ca. 1 mm long. Calyx lobes triangular with acuminate apices, 1–1.5 by 0.6–1 mm, abaxial surface essentially glabrous; corolla cylindrical, 7–8 by 2.5–3.5 mm, white, abaxially glabrous; filaments 4.5–5 mm long, anthers 1.1–1.2 mm long; ovary glabrous to moderately pubescent, placentae ± subapical(?). Capsules not seen.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, Minas Gerais (MAP 9). Open sandy or rocky areas; ca. 1300 m alt. Flowering October to December.

REPRESENTATIVE SPECIMEN. **Brazil.** MINAS GERAIS: Serra do Cipó, Sta. Ana do Riacho, *Hatschbach & Koczicki 35379* (L).

This rare and little-collected species is most closely related to *Agarista angustissima* and *A. glaberrima.* It is easily distinguished from both of these species by its often pubescent stems and inflorescence axis, its shorter petioles, and its shorter and exclusively axillary racemes. Its leaves, like those of *A. angustissima,* are linear and very strongly adaxially folded. *Agarista duartei*

has only been collected in the Serra do Cipó, a region where the genus shows a large amount of diversity. Fruiting material has not been seen.

Agarista D. Don ex G. Don sect. **Agauria** (DC.) Judd, comb nov.

Leucothoë D. Don sect. *Agauria* DC. Prodr. **7:** 602. 1839. *Agauria* (DC.) J. D. Hooker *in* Bentham & Hooker, Gen. Pl. **2:** 586. 1876. LECTOTYPE SPECIES: *Agarista salicifolia* (Comm. ex Lam.) G. Don.

Twigs with nonchambered, slightly to very heterogeneous pith. Leaves with the abaxial epidermis papillose, the adaxial epidermal cells short, usually not divided. Style apparently not swollen. Capsules with placentae basal; seeds 3–4 mm long.

DISTRIBUTION. Central Africa, Madagascar, Réunion, and Mauritius (see Sleumer, 1938, *fig. 1*).

NUMBER OF SPECIES (TAXA): 1 (20).

This section is not treated here; see Sleumer (1938) for a revision of the group and a key to the many infraspecific taxa comprising the widespread and variable *Agarista salicifolia* (species no. 30).

SPECIES EXCLUDED FROM AGARISTA

Agarista anastomosans G. Don, Gen. Syst. **3:** 838. 1834, nomen superfl. = **Gaultheria glomerata** (Cav.) Sleumer (Sleumer, 1959).
Agarista ciliata (Nees) J. D. Hooker ex Niedenzu, Bot. Jahrb. **11:** 236. 1889 = **Gaylussacia brasiliensis** (Sprengel) Meissner (Sleumer, 1959).
Agarista coccinea (Schrader) J. D. Hooker ex Niedenzu, *ibid.* = **Gaylussacia brasiliensis** (Sprengel) Meissner (Sleumer, 1959).
Agarista eriophylla (Pers.) G. Don, Gen. Syst. **3:** 838. 1834 = **Gaultheria eriophylla** (Pers.) Sleumer ex Burtt (Sleumer, 1959).
Agarista ilicifolia (Pers.) G. Don, Gen. Syst. **3:** 838. 1834 = **Gaultheria phillyreifolia** (Pers.) Sleumer (Sleumer, 1959).
Agarista itatiaiae (Wawra) Wawra, Itin. Princ. Coburgi **1:** 73. 1883 = **Gaultheria itatiaiae** Wawra (Sleumer, 1959).

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THE TRIBES OF CRUCIFERAE (BRASSICACEAE) IN THE SOUTHEASTERN UNITED STATES[1]

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The family Cruciferae is represented in the southeastern United States by 121 species in 43 genera assigned to seven tribes. The present account includes a family description, with general comments on the group as a whole; selected family references; a key to the tribes; an artificial key to 46 genera (including three known as escapes from cultivation to the west of this area); and brief descriptions of the tribes, each with a list of the representative genera in the Southeast.

When treating a family generally recognized as difficult for generic and tribal delimitation, one faces the problem of how genera should be arranged. An alphabetic sequence would definitely be incompatible with the scope of our flora. A few students of the family avoid recognizing tribes because they believe that tribal boundaries are usually artificial. However, these authors arrange the genera according to their nearest sister relatives—a disposition that often coincides so well with the tribal classification that ignoring or totally abandoning the tribes is unreasonable. Nearly half of the genera of Cruciferae occurring in our area belong to the tribes Thelypodieae, Brassiceae, and Lepidieae, which are widely recognized as natural groups. The majority of the remaining genera fall within the presumably well-defined centers of four other tribes. For these reasons I favor the use of tribes to provide a workable framework, even though

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I fully admit that, when taken on a worldwide basis, some tribal boundaries become clearly artificial.

CRUCIFERAE A. L. de Jussieu, Gen. Pl. 237. 1789.

Nom. alt. BRASSICACEAE Burnett, Outlines Bot. 1123. 1835.

(MUSTARD FAMILY)

Annual, biennial, or perennial herbs [rarely vines, subshrubs, shrubs, or even small trees], with pungent, watery juice rich in glucosinolates (mustard-oil glucosides) and with idioblasts containing myrosinase; indumentum lacking or of simple, furcate, dendritic, or stellate unicellular, eglandular trichomes, very rarely with additional unicellular or multicellular glands. Leaves alternate [very rarely opposite], sometimes confined to a basal rosette, exstipulate, simple, very rarely pinnate or palmate, as in *Cardamine*; stomata typically anisocytic, rarely mixed with few of some other types. Inflorescences terminal (axillary in *Coronopus*), usually racemes, corymbs, or panicles, rarely solitary on long scapes (*Leavenworthia*), usually ebracteate (bracteate in *Selenia*). Flowers hypogynous, actinomorphic (zygomorphic in *Teesdalia*), perfect [very rarely imperfect]. Sepals 4, almost always free, in 2 decussate pairs, mostly deciduous; inner (lateral) pair often saccate [rarely spurred]. Petals 4, rarely absent, free, alternating with the sepals, usually clawed, arranged in the form of a cross (cruciform, hence the family name), imbricate or contorted [rarely circinate] in bud, entire [rarely lobed, pinnatifid, or fimbriate]. Stamens 6, tetradynamous (the outer 2 shorter than the inner 4), rarely equal in length (*Warea*) or in 3 pairs of unequal length (*Streptanthus*), sometimes 2 or 4 (*Lepidium*) [very rarely 8–24, as in *Megacarpaea polyandra*]; filaments filiform, sometimes winged or appendaged at the base, free [or those of the median pairs of stamens sometimes connate]; anthers 4-sporangiate, 2-loculate at anthesis; pollen grains tricolpate (5- to 7-colpate in *Lesquerella*) [or up to 10-colpate in *Dimorphocarpa*], usually oblate or prolate, reticulate, trinucleate when shed. Nectar glands receptacular in origin, highly diversified in shape, size, and disposition around the bases of filaments. Gynoecium 2-carpellate, syncarpous; style persistent, distinct or obsolete; stigma terminal, capitate or discoid, entire or 2-lobed, the lobes opposite the placenta (replum), rarely opposite the valves, sometimes decurrent and/or connate along entire length; ovary superior, usually sessile (long-stipitate in *Warea*), 2-loculate, rarely uniloculate, with a false septum connecting the 2 parietal (or rarely subapical) placentae; ovules anatropous or campylotropous, 2-integumented, crassinucellate or tenuinucellate, few to many (sometimes 1) per locule. Fruit typically a bivalvate capsule dehiscing longitudinally from below (commonly called a silique (siliqua) when more than 3 times longer than broad, or a silicle (silicula) when clearly shorter than 3 times the width, but such distinctions arbitrary and sometimes misleading), or fruit indehiscent and becoming lomentaceous or achenelike [or a nutlet, samara, schizocarp, or even a drupe], usually beakless, or having seedless or 1- to few-seeded beaks; replum (the framelike placenta) persistent; septum complete (incomplete or reduced to a rim in *Armoracia*), usually membranaceous [rarely thick and fibrous or

nerved]; gynophores generally lacking or very short (well developed in *Warea* and *Lunaria*). Seeds without endosperm, uniseriately or biseriately arranged, winged or wingless, mucilaginous or not when wet; megagametophyte (embryo sac) of the Polygonum type; embryogeny of the Onagrad type; embryo oily, occupying the entire seed, strongly curved (straight only in *Leavenworthia*) or folded in one of seven ways, most commonly notorrhizal (cotyledons incumbent—i.e., radicle lying on the back of 1 cotyledon), pleurorrhizal (cotyledons accumbent—radicle applied to the margin of both cotyledons), or orthoplocal (cotyledons conduplicate—folded longitudinally around the radicle) [or diplecolobal—cotyledons twice transversely folded]; germination epigeal. $x = 4–13$. (Including Raphanaceae Horan., Cruciaceae Dulac.) TYPE GENUS: *Brassica* L.

A large family of approximately 340 genera and more than 3350 species in some ten poorly defined tribes, distributed throughout the world, primarily in the temperate regions and most successfully in the arid areas (although a few species of *Draba* and of some other genera have penetrated well into the Arctic and to the subantarctic islands, while others grow at altitudes of up to 6000 meters (19,700 feet) in Kashmir and Tibet). The family is clearly most abundant in the Northern Hemisphere, with the major center of diversification and endemism in the Irano-Turranian region, where some 150 genera (62 endemic) and 900 species (530 endemic) are found, and a secondary center in the Mediterranean region, with more than 110 genera (21 endemic) and nearly 630 species (290 endemic). Most of the 37 endemic genera and more than 600 species native to North America are distributed primarily in the western United States and northern Mexico. In the Southern Hemisphere, there are 32 endemic genera and some 340 species native to South America (particularly along the Andes and in Patagonia), eight genera and 110 species in South Africa, and 19 genera and 114 species in Australia and New Zealand. Only two genera (*Romanschulzia* O. E. Schulz of Mexico and Central America and *Oreophyton* O. E. Schulz of eastern tropical Africa) are endemic to the high mountains of the tropics. Of all the genera in the family, only *Cardamine* L., *Lepidium* L., and *Rorippa* Scop. are represented by indigenous species on all continents but Antarctica. Of the 121 species occurring in the southeastern United States, 55 (falling in 27 genera) are naturalized weeds, most of which were originally introduced from Europe. The majority of our 66 native species occur elsewhere in eastern North America, but only 16 of them are endemic to the Southeast, and six others have their centers of distribution in our area. Only one genus (*Warea* Nutt.) is endemic, and another (*Leavenworthia* Torrey) has its center of diversity in the Southeast. Seven of the nine taxa of *Cakile* Miller native to North America occur in our area, but the genus apparently originated and has diversified in the Old World (southwestern Asia and Europe).

A very natural family easily distinguished by the cruciform corolla, the tetradynamous stamens, and the characteristic siliques (hereafter to include the silicle), the Cruciferae—whether placed in the order Capparales of recent authors or in the abandoned Englerian Rhoeadales (see Wettstein)—have always been closely associated with the Capparaceae. Systematists are now in agreement that the Rhoeadales represent two unrelated orders, the Capparales (containing glucosinolates, myrosin cells, and centrifugal stamens, and lacking

laticifers and benzylisoquinoline alkaloids) and the Papaverales (with benzylisoquinoline alkaloids, laticifers, and centripetal stamens, and lacking glucosinolates and myrosin cells) (see Gershenzon & Mabry; Rodman, 1981). The family has recently been considered to be a direct descendant from the capparaceous subfamily Cleomoideae via the cruciferous tribe Stanleyeae (= Thelypodieae) (Janchen; Takhtajan) or through the Hesperideae (Dvořák, 1973). Although the morphological evidence very strongly favors a connection through the Thelypodieae, none of the extant crucifers is truly archaic, and the palynological data (Al-Shehbaz, 1973) do not support such a direct link. It is, therefore, more reasonable to assume that the connection between the two families is through a common ancestor. Fossil evidence is of no help here, and the few scattered reports of cruciferous pollen from the Upper Miocene of France (Muller) and the Cretaceous of New Zealand (Couper), as well as the fossil siliques of *Thlaspi* L. from the Oligocene of Montana (Becker) and those of *Lepidium* and other genera (Schulz), only complicate the problem.

The tribal classification of the family has occasioned more controversy than any other aspect of its systematics, and none of the existing tribal systems comes close to satisfying all concerned. Although much criticized for its artificiality, Schulz's is the latest comprehensive monograph on the family, and despite its weaknesses, his system is the most widely followed. With the exception of the tribes Brassiceae, Lepidieae, and Thelypodieae (the Stanleyeae, Streptantheae, and Romanschulzieae of Schulz), all the other large tribes of his system fall short of being natural. Janchen reduced the 19 tribes of Schulz to 15, and his merging of the Matthioleae with the Hesperideae and of both the Drabeae and Lunarieae with the Alysseae is probably justified. The Cremolobeae R. Br. (two genera and 36 species of South America) and the Heliophileae DC. (four genera and 77 species of South Africa) are sufficiently distinct and probably merit recognition, but the tribal status of the Pringleeae Hayek and Chamireae Sonder, both unigeneric and monotypic, needs careful evaluation. On the other hand, the Stenopetaleae O. E. Schulz, an Australian unigeneric tribe with eight species, rest solely on the narrowly linear or filiform petals that are circinate in bud, a feature independently evolved in the unrelated Australian monotypic *Carinavalva* Ising and the North American *Lyrocarpa* Hooker & Harvey. The genera of the Schizopetaleae R. Br. ex Barn., *Schizopetalon* Sims (seven species, Chile), *Ornithocarpa* Rose (two species, Mexico), and *Dryopetalon* Gray (four species, northwestern Mexico and the adjacent United States), are united mainly by the divided petals. However, they are so different in their fruits, sepal orientation, indumentum, nectaries, stigmas, and cotyledons that they form a highly heterogeneous group of unrelated genera (see Rollins, 1969). In my opinion, each of these genera can be loosely associated with certain members of one of three other tribes.

Avetisian (1976, 1983) has recently reduced Schulz's tribes to three, Thelypodieae, Brassiceae, and Sisymbrieae, but such an action does not seem to be well founded. In the past, tribes have been erected on the basis of differences in a few characters such as cotyledonary position, type of pubescence, and fruit length and the type of its flattening, but this always leads to artificiality in the tribal classification. Perhaps a more realistic classification of the family can be

achieved by grouping the closely related genera and working upward to more natural infrafamilial taxa. The modified version of Janchen's system adopted here is only intended to provide a workable framework for infrafamilial subdivisions above the generic level, but even though it represents a major improvement over Schulz's system, it cannot be considered natural as far as the tribal limits of the Alysseae, Arabideae, Hesperideae, and Sisymbrieae are concerned. Generic boundaries in the family are often arbitrarily drawn, and the establishment of clear-cut intergeneric relationships is often difficult. Although there is an average of about ten species to a genus, the majority of genera (250) are oligotypic with five or fewer species, and 138 of these are monotypic. However, more than half of the species of the family belong to 12 large genera: *Draba* L. (340), *Erysimum* L. (180), *Cardamine* (175), *Lepidium* (175), *Alyssum* L. (170), *Arabis* L. (170), *Sisymbrium* L. (90), *Lesquerella* S. Watson (80), *Rorippa* (75), *Thlaspi* (75), *Heliophila* L. (72), and *Hesperis* L. (60). Unlike many of the small genera, the species are generally very distinct throughout the family. A few exceptions, however, do exist, and the most notable examples are the Old World genera *Isatis* L., *Aethionema* R. Br., and *Biscutella* L., in which hybridization, polyploidy, and apomixis, alone or together, may have played an important role in making species determination a very difficult task.

Chromosome numbers have been reported for more than 1400 species (41% of the family total) in 197 genera (author's compilation). A continuous series of base chromosome numbers from four to 13 exists, but a surprisingly high percentage (37%) of the species appear to be based on eight. The lowest chromosome number known for the family ($n = 4$) has been found so far only in two unrelated genera, the Australian *Stenopetalum* R. Br. ex DC. and the western North American *Physaria* (Nutt.) Gray, while the highest number reported ($n = 128$) is in *Cardamine laciniata* (Muhl. ex Willd.) Wood. Nearly 37 percent of the species are polyploid, and some of the genera such as *Crambe* L. (Brassiceae) and *Streptanthus* Nutt. (Thelypodieae) appear to be exclusively polyploid. Both genera are generally considered the most advanced in their respective tribes. However, Mukherjee believes that aneuploidy and diminution in chromosome size, rather than polyploidy, have played an important role in the evolution of the family. The tribes Alysseae and Arabideae have a base chromosome number of eight, which has been found in more than 60 percent of their species; only about 10–15 percent of their species are based on seven. On the other hand, the tribes Hesperideae, Lepidieae, and Sisymbrieae are based primarily on seven, which has been found in about 40–45 percent of their species, and secondarily on eight, encountered in about 20 percent of the species of each tribe. No single base chromosome number dominates in the Brassiceae, and with more than 77 percent of its species known cytologically, the base numbers 7, 8, 9, 10, 11, 12, and 15 occur with frequencies ranging from eight to 20 percent. Although the Thelypodieae have a continuous series of haploid chromosome numbers of ten to 15 (with nearly 46 percent of the species known cytologically), $n = 14$ occurs in more than 60 percent of the species and $n = 13$ in about 20 percent.

Many genera of the Cruciferae have been studied for their chemical con-

stituents, especially the glucosinolates (mustard-oil glucosides) and the seed fatty acids, both of which have been thoroughly surveyed in the economic species and their wild allies. The fatty-acid composition is known for at least 165 species in 70 genera; in this small sample, the linolenic or erucic acids are the most dominant constituents in the seeds of about 85 percent of the species surveyed. All Cruciferae appear to have glucosinolates, and of the approximately 85 types known, only methyl glucosinolate (typically characteristic of the Capparaceae) has not been found in any crucifer (see Hedge *et al.*). The distribution of these compounds has been shown to be a valuable tool in chemosystematic studies at the generic and specific levels (Rodman, 1981). In all, some 350 species in about 70 genera have been surveyed, but since most of the earlier reports have dealt only with the distribution of the major constituents, many of the species need to be reinvestigated in order to have a complete profile of their glucosinolates. It is agreed that the glucosinolates probably play the most important role in the chemical defense of crucifers against pathogens and herbivores. Research on the distribution of the fatty acids or the glucosinolates has so far failed to provide any meaningful support for the tribal classification of the family. The flavonoid chemistry in the family has not received the attention it deserves, and some of the recent works (Bacon) show that such compounds can be equally valuable in systematic studies in this family. Other secondary metabolites generally occur in negligible amounts, and they are often overlooked. However, relatively high concentrations of alkaloids (*Lunaria* L.), cucurbitacins (*Iberis* L.), and cardenolides (*Erysimum*) may be found, and the distribution of the last group of compounds may prove to be useful in solving some of the problems in taxonomically difficult genera such as *Erysimum*. Species of a few genera are known to accumulate high amounts of selenium (*Stanleya* Nutt.) or nickel (*Alyssum, Streptanthus*), but these capacities have no taxonomic value.

Floral anatomy in the Cruciferae has been studied in detail, mainly to resolve several controversial aspects of the gynoecial structure, such as the vasculature of the ovary, the number of carpels, the origin of the septum, the position of the stigmatic lobes, and the derivation of the placentae. The widely accepted bicarpellary hypothesis advocated by Arber, Zohary (1948b), Puri (1951), and Alexander states that the cruciferous gynoecium originated through the connation of the margins of two lateral carpels to form two median parietal placentae, each of which produces an outgrowth that fuses with the other in the center to form the false septum. This hypothesis, however, fails to provide an adequate explanation for the inverted position of the inner vascular bundles of the replum and for the frequent commissural position of the stigma lobes. The tetracarpellary views of Saunders, Eames & Wilson, Puri (1941), Merxmüller & Leins, and (more recently) Eigner agree that the cruciferous gynoecium is composed of four carpels, of which the median two are fertile and the lateral two are sterile. Despite the fact that these hypotheses provide sound interpretation for the vasculature of the stigma and replum, they do not adequately explain the origin of the false septum and the position of the ovules. Furthermore, as indicated by Zohary (1948b), in crucifers with dehiscent fruits, the lines of dehiscence appear only in the later stages of development and do not

correspond with carpel margins, as proposed by Saunders and others (see above). Although I support the bicarpellary interpretation and believe that the gynoecium of the Cruciferae is homologous to that of the closely related Capparaceae, both the bi- and tetracarpellary views fail to provide fully satisfactory answers for all the various aspects of the cruciferous gynoecium. The reader is advised to consult Maule and Roth for further details.

Flower colors of Cruciferae are predominantly yellow, white, and shades from lavender to purple; true blue or red flowers, if they occur at all, are indeed very rare. The remarkable constancy of floral architecture in the family has been very closely linked to pollination by insects, particularly various Hymenoptera, Diptera, Lepidoptera, and some Coleoptera. Wind pollination is extremely rare and is probably best known in *Pringlea antiscorbutica* R. Br., a species restricted to the small Kerguelen and Crozet islands of the southern Indian Ocean. Autogamy is common in many of the weedy species, while cleistogamy always occurs in the submersed plants of *Subularia aquatica* L. Unlike protogyny, protandry appears to be rare in the family (Al-Shehbaz, 1977), and except for very few examples, the flowers of the Cruciferae are almost always perfect. Dioecism is known in three species of *Lepidium* from New Zealand, while monoecism has been reported in *Megacarpaea megalocarpa* (Fischer ex DC.) Schischkin ex Fedtsch., of central Asia and southeastern Russia.

Fruits of the Cruciferae are so diverse that they are the most reliably used structures for the proper identification of genera and species. In plants with dehiscent siliques, seed dispersal—even if explosive, as in *Cardamine*—is confined to short distances from the parent plant. However, because of their small size, seeds of the family in general are easily washed farther away by rain or transported by strong winds in open habitats. The corky fruits of all but one of the taxa of *Cakile* and of some species of *Crambe* and *Raphanus* L. are transported by sea, while the winged seeds and samaroid and bladdery fruits that have independently evolved many times in the family are dispersed by wind. The dustlike seeds of certain Saharan species of *Diplotaxis* DC. may weigh as little as 0.05 mg and can therefore be transported by storms for several hundred miles. The remarkable rose of Jericho (tumbling or resurrection mustard), *Anastatica hierochuntica* L., is dispersed by the tumbling of the entire dry plant, and this species has a continuous distribution extending 8000 kilometers (5000 miles) in hot deserts from Mauretania to western Pakistan. Fruit dispersal by mammals is known for several genera having hooked hairs (*Tauscheria* Fischer ex DC.), glochidiate spines (*Clypeola* L.), and other adaptive features. Geocarpy has evolved independently in the Australian *Geococcus pusillus* Drumm. ex Harvey, in the South American *Cardamine chenopodiifolia* Pers., and in *Morisia monanthos* (Viv.) Ascherson, of Corsica and Sardinia.

The family is primarily herbaceous, and only some five percent of its species are typically woody; more than 62 percent are perennials. Growth forms, however, may vary from delicate annual herbs to the South American hummock-forming *Xerodraba pycnophylloides* (Spegaz.) Skottsb. and *Lithodraba mendociensis* (Spegaz.) Boelcke, the South African woody climber *Heliophila scandens* Harvey, the large shrubs *Foleyola* Maire of northern Africa and *Par-*

olinia Webb of the Canary Islands, or even the small tree *Farsetia somalensis* (Pax) Gilg & C. Benedict, of Somalia, Ethiopia, and Kenya. *Farsetia* Turra also contains a few annual or perennial herbs, which may be less than 10 cm high, as well as large shrubs that may exceed 2 m in height in eastern tropical Africa. Typical shrubs are found in about two percent of the total species of Cruciferae in at least 16 genera scattered in different tribes. The woody condition appears to be almost always a derived one, and it must have evolved independently many times within the family.

The family includes a number of important crop plants that are grown as food for humans or animals, as sources of condiments or edible and industrial oils, or as ornamentals. The family is also known for its more than 120 weedy species of local or cosmopolitan distribution that invade cultivated lands and occupy disturbed sites, roadsides, waste grounds, and the like. *Brassica* is the most important genus, for it contains several vegetable and salad plants such as cabbage, cauliflower, Brussels sprouts, kale, broccoli, kohlrabi (all considered to be varieties of *B. oleracea* L.), turnip and Chinese cabbage (*B. campestris* L.), rape (*B. napus* L.), Chinese or Indian mustard (*B. juncea* (L.) Czern.), and black mustard (*B. nigra* (L.) W. D. Koch). Other crops include the radish (*Raphanus sativus* L.), watercress (*Nasturtium officinale* R. Br.), and the common or garden cress (*Lepidium sativum* L.). Condiments are obtained from the fleshy roots of horseradish (*Armoracia rusticana* Gaertner, Meyer, & Scherb.), while table mustard is prepared from a mixture of the seeds of the white mustard (*Sinapis alba* L.) and those of either the black or the Indian mustard.

Oils from crucifer seeds, particularly from rape, rank fifth in terms of the world tonnage production, and most of it (except that used for making margarine in Europe and cooking oil in India) is utilized in the manufacture of numerous industrial products. The seed cake remaining after the expression of oil is rich in protein, and until recently it has been extensively used as feed for farm animals. It contains potentially harmful mustard oils, however, so this usage has become very limited, and most of the seed cake is now used as a fertilizer.

The most important ornamental crucifers include the wallflower (*Erysimum Cheiri* (L.) Crantz, rocket or dame's violet (*Hesperis matronalis* L.), candytuft (*Iberis* species), honesty or money plant (*Lunaria annua* L. and *L. rediviva* L.), sweet alyssum (*Lobularia maritima* (L.) Desv.), stock (*Matthiola incana* (L.) R. Br.), aubrietia (*Aubrieta deltoidea* (L.) DC.), rock cress (*Arabis* species), and some species of the genera *Aethionema, Alyssum, Brassica,* and *Draba.* The historic blue dye woad was obtained from the fermented ground leaves of *Isatis tinctoria* L.

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KEYS TO THE TRIBES AND GENERA OF CRUCIFERAE IN THE SOUTHEASTERN UNITED STATES

General characters: *Mostly annual, biennial, or perennial herbs, rarely shrubs, glabrous or with simple or variously branched unicellular trichomes, rarely with multicellular glandular trichomes; leaves exstipulate, usually simple, alternate; inflorescences basically racemes or corymbs (flowers rarely solitary), usually ebracteate; flowers hypogynous, mostly actinomorphic, perfect; sepals 4, in 2 decussate pairs, erect or spreading, the lateral (inner) pair often saccate at the base; corolla cruciform, the petals 4, usually clawed, rarely absent; nectar glands receptacular, surrounding or subtending the bases of some or all filaments; androecium of 6 stamens (rarely 2, 4, or more than 6) in 2 whorls, the outer pair usually shorter than the 2 inner pairs (tetradynamous), rarely all equal in length; gynoecium of 2 united carpels; ovary superior, often 2-locular by a false septum connecting the 2 parietal placentae; style persistent, distinct or obsolete; stigma entire or 2-lobed; ovules 1 to many, anatropous or campylotropous; fruit basically a capsule (often called a silique), dehiscing longitudinally by 2 valves, sometimes indehiscent and modified to a loment, nutlet, samara, or schizocarp; seeds without endosperm, winged or wingless, mucilaginous or not when wet; embryos large, almost always folded or curved in one of several ways.*

Key to the Tribes

A. Fruits mostly beaked, sometimes transversely jointed and breaking at maturity into 2 or more seed-bearing segments; beak 1- or few-seeded, rarely seedless; cotyledons almost always conduplicate. . . . . Tribe 2. BRASSICEAE.

A. Fruits beakless or very rarely with a seedless stylelike beak, never jointed; cotyledons accumbent or incumbent.

B. Fruits strongly compressed at right angles to the septum; replum much narrower than width of fruit. . . . . Tribe 3. LEPIDIEAE.

B. Fruits terete, angular, inflated, or compressed parallel to the septum; replum equaling width of fruit.
C. Fruits less than 3 times longer than broad (except in a few species of *Draba*); plants mostly with stellate or furcate trichomes, with or without unbranched ones. . . . . Tribe 4. ALYSSEAE.
C. Fruits mostly more than 3 times longer than broad, if less the plants (ours) glabrous; trichomes branched, unbranched, or absent.
D. Stamens mostly exserted, equal in length, sometimes slightly tetradynamous, or in 3 pairs of unequal length; petals mostly crisped or channeled; gynophores (1–)2–30 mm long; trichomes simple or absent. . . . . Tribe 1. THELYPODIEAE.
D. Stamens included or slightly protruding, tetradynamous; petals usually neither crisped nor channeled; gynophores absent or rarely present, to 2 mm long; trichomes branched, simple, or lacking.
E. Sepals erect, calyx closed at anthesis; multicellular glandular trichomes commonly present. . . . . Tribe 6. HESPERIDEAE.
E. Sepals spreading or ascending, calyx open at anthesis; multicellular glands always absent.
F. Cotyledons accumbent. . . . . Tribe 5. ARABIDEAE.
F. Cotyledons incumbent. . . . . Tribe 7. SISYMBRIEAE.

Key to the Genera

Several species of *Iberis* L. (candytuft), *Malcolmia* R. Br. (Virginian stock), and *Matthiola* R. Br. (stock) are cultivated in our area, but there are no records that any of them has become naturalized. *Malcolmia africana* (L.) R. Br. and *Matthiola longipetala* (Vent.) DC. are well-established weeds in Texas and some of the western states, but neither of them has been found in our area. These three genera are included in the following key, but they will not be dealt with further.

A. Fruits transversely jointed or lomentaceous, indehiscent, often breaking transversely at maturity into 1- or few-seeded segments.
B. Plants with stalked, multicellular, glandular trichomes; fruits not transversely jointed; stigmas with strongly decurrent connate lobes. . . . . 37. *Chorispora.*
B. Plants eglandular, glabrous or with simple, unicellular trichomes only; fruits transversely jointed; stigmas entire or 2-lobed—if 2-lobed, lobes neither decurrent nor connate.
C. Lower segment of fruit always seedless; upper segment several seeded, more than 10 times longer than the lower segment. . . . . 9. *Raphanus.*
C. Lower segment of fruit usually 1-seeded, rarely 3-seeded or seedless; upper segment 1- or rarely 2-seeded, equaling or up to 5 times longer than the lower segment.
D. Petals yellow; fruits not corky, less than 1 cm long; cotyledons conduplicate; hirsute, nonfleshy weeds of waste grounds and cultivated land. . . . . 10. *Rapistrum.*
D. Petals white, or lavender to purple; fruits corky, often more than 1.5 cm long; cotyledons accumbent, rarely incumbent; glabrous, often fleshy plants of sandy shores or beaches. . . . . 12. *Cakile.*
A. Fruits neither jointed nor lomentaceous, dehiscent or rarely indehiscent (*Calepina*), not breaking transversely into segments.
E. Early flowers solitary, borne on scapes 3–10 cm long originating from center of a basal rosette; radicles straight or slightly curved, much shorter than cotyledons. . . . . 30. *Leavenworthia.*
E. All flowers borne in terminal or axillary racemes or corymbs; radicles strongly curved, about as long as the accumbent, incumbent, or conduplicate cotyledons.

F. Fruits less than 3 times longer than broad, broadly oblong or elliptic to globose, orbicular, triangular, or didymous.
G. Fruits strongly compressed at right angles to the septum; replum much narrower than width of fruit.
H. Flowers zygomorphic; outer petals markedly larger than inner.
I. Seed 1 in each locule; median filaments not appendaged. . . . . [*Iberis.*]
I. Seeds 2 in each locule; median filaments with a broad, scalelike appendage. . . . . 18. *Teesdalia.*
H. Flowers actinomorphic; petals equal in size, sometimes reduced or lacking.
J. Seeds 3 or more, rarely 2 per locule.
K. Fruits obcordate-triangular; basal leaves forming a rosette; plants with furcate and stellate trichomes. . . . . 19. *Capsella.*
K. Fruits orbicular or elliptic; basal leaves not in rosettes; plants glabrous or with unbranched trichomes only. . . . 17. *Thlaspi.*
J. Seed 1 per locule.
L. Fruits coarsely reticulate or verrucose, often didymous; inflorescence axillary; upper cauline leaves 1- or 2-pinnatisect. . . . . 15. *Coronopus.*
L. Fruits smooth; inflorescence terminal; upper cauline leaves entire, toothed, or pinnately lobed.
M. Fruits dehiscent, obtuse or cuneate at base, retuse or emarginate at apex; annuals, biennials, or nonstoloniferous perennials. . . . . 14. *Lepidium.*
M. Fruits indehiscent, cordate at base, cuneate at apex; stoloniferous perennials. . . . . 16. *Cardaria.*
G. Fruits inflated, globular, or compressed parallel to the septum; replum about as broad as width of fruit.
N. Plants glabrous or pubescent with unbranched trichomes only.
O. Fruits coarsely reticulate-rugose, ribbed, indehiscent, 1-seeded; petals unequal; cotyledons conduplicate. . . . . 11. *Calepina.*
O. Fruits smooth, not ribbed, dehiscent, many seeded; petals equal; cotyledons accumbent.
P. Fruits strongly compressed parallel to the septum; seeds compressed, broadly winged, 3–10 mm wide.
Q. Flowers purple, rarely white; inflorescence ebracteate; leaves dentate; fruits more than 1.5 cm broad; gynophores 1–3 cm long; funiculi united with the septum. . . 20. *Lunaria.*
Q. Flowers yellow; inflorescence bracteate throughout; leaves pinnatisect; fruits less than 1 cm broad; gynophores less than 0.5 cm long; funiculi free from the septum. . . . . 31. *Selenia.*
P. Fruits inflated; seeds plump, wingless, less than 1.5 mm wide.
R. Flowers white; septum rudimentary or incomplete; plants perennial. . . . . 36. *Armoracia.*
R. Flowers yellow; septum complete; plants annual or biennial, rarely perennial. . . . . 35. *Rorippa.*
N. Plants pubescent with furcate, branched, or stellate trichomes, and with or without unbranched ones.
S. All trichomes uniformly bifurcate, medifixed, appressed, sessile. . . . . 22. *Lobularia.*
S. Trichomes stellate, furcate, or branched, mixed with unbranched ones or not, stalked, sometimes sessile and appressed when stellate.

T. Petals deeply bilobed.
U. Plants scapose; fruits glabrous; filaments of lateral stamens not appendaged; styles obsolete. ..... 24. *Draba.*
U. Plants not scapose; fruits densely pubescent; filaments of lateral stamens appendaged; styles 1.5–4 mm long. ..... 23. *Berteroa.*
T. Petals entire or slightly emarginate.
V. Fruits orbicular or oblong to lanceolate, often strongly compressed.
W. Seeds wingless, biseriate, usually more than 4 per locule; fruits oblong or lanceolate. ..... 24. *Draba.*
W. Seeds winged or margined, uniseriate, 1–4 per locule; fruits orbicular or nearly so.
X. Cauline leaves cuneate, not auriculate; styles less than 1 mm long; seed 1 per locule, strongly mucilaginous when wet. ..... 21. *Alyssum.*
X. Cauline leaves auriculate; styles 1.5–3 mm long; seeds 2–4 per locule, not mucilaginous when wet. ..... 25. *Lesquerella.*
V. Fruits globose or pyriform, inflated.
Y. Fruits globose, not keeled, beakless; valve apex obtuse, ending at base of style; seeds usually orbicular; cotyledons accumbent. ..... 25. *Lesquerella.*
Y. Fruits pyriform, keeled at the replum, ending abruptly in a stylelike beak; valve apex acuminate, extending 0.5–1.5 mm into the beak area; seeds usually oblong; cotyledons incumbent. ..... 26. *Camelina.*
F. Fruits at least 4 times longer (often much more) than broad, linear or narrowly oblong.
a. Plants with forked, branched, dendritic, or stellate trichomes, sometimes mixed with unbranched ones.
b. Leaves 2- or 3-pinnatisect. ..... 43. *Descurainia.*
b. Leaves entire to pinnately lobed, never 2-pinnatisect.
c. Stigmas with strongly decurrent lobes.
d. Stigma lobes with a lateral horn or swelling in fruit. ..... [*Matthiola.*]
d. Stigma lobes without an outgrowth.
e. Annuals; stigma lobes connate along their entire length in fruit; fruits sharply pointed. ..... [*Malcolmia.*]
e. Biennials; stigma lobes free in mature fruits; fruits not pointed. ..... 38. *Hesperis.*
c. Stigmas capitate, entire or 2-lobed (if 2-lobed, lobes shallow, divergent, never decurrent).
f. Trichomes appressed, medifixed, bifurcate mixed with 3–5-furcate or stellate ones, never unbranched; fruits mostly quadrangular in section. ..... 39. *Erysimum.*
f. Trichomes a mixture of 2 kinds: unbranched and stalked furcate; fruits terete or flattened parallel to the septum.
g. Fruits terete; cotyledons incumbent. ..... 42. *Arabidopsis.*
g. Fruits flattened; cotyledons accumbent.
h. Plants scapose; fruits less than 2 cm long, less than 6 times longer than broad; seeds clearly biseriately arranged. ..... 24. *Draba.*
h. Plants not scapose; fruits mostly more than 2 cm long, more

than 10 times longer than broad; seeds uniseriately arranged, very rarely obscurely biseriate. ..... 32. *Arabis.*

a. Plants glabrous or with unbranched trichomes only.
i. Stamens long-exserted, equal in length; sepals strongly reflexed; petal claws papillose near the base; gynophores (3–)5–14 mm long. ..... 1. *Warea.*

i. Stamens included or slightly protruding, tetradynamous or in 3 pairs of unequal length; sepals erect or spreading, very rarely reflexed; petal claws glabrous; gynophores absent or very rarely present, to 3 mm long.
j. Fruits with a strongly developed beak in addition to style, rarely obscurely beaked (*Diplotaxis* and *Erucastrum*); cotyledons always conduplicate.
k. Valves with 1 prominent midnerve, with or without a few inconspicuous lateral veins.
l. Inflorescence bracteate; fruits 4-angled. ..... 4. *Erucastrum.*
l. Inflorescence ebracteate; fruits terete or flattened.
m. Beaks strongly flattened, ensiform; stigma lobes decurrent; petals with dark brown or purple veins. ..... 8. *Eruca.*
m. Beaks conical or stylelike; stigmas entire or with nondecurrent lobes; petal veins not darkly colored.
n. Fruits flattened; seeds biseriately arranged, ovoid or oblong, up to 1.5 mm long. ..... 7. *Diplotaxis.*
n. Fruits terete; seeds uniseriately arranged, globose, 1.5–2.5 mm in diameter. ..... 3. *Brassica.*
k. Valves with 3–7 prominent nerves (these often more conspicuous on immature fruits).
o. Sepals erect, saccate at the base; petal claws as long as or longer than the sepals. ..... 5. *Hutera.*
o. Sepals widely spreading or reflexed, not saccate; petal claws shorter than the sepals. ..... 6. *Sinapis.*
j. Fruits beakless; cotyledons accumbent or incumbent.
p. Fruits flattened parallel to septum; petals never yellow.
q. Valves dehiscing suddenly and elastically from the base, coiling circinately or spirally; replum flanged with remains of valve margin; seeds neither winged nor margined; plants perennials with tubers or rhizomes, sometimes annuals or biennials. .. .. 27. *Cardamine.*
q. Valves not dehiscing elastically, not coiling; replum margin not flanged; seeds winged or margined, very rarely wingless; plants (ours) annuals or biennials.
r. Cauline leaves all pinnatisect or pinnatifid. ...33. *Sibara.*
r. Cauline leaves entire or toothed.
s. Petals showy, purple to magenta, rarely lavender, crisped, 1–2 cm long, differentiated at base into an oblanceolate claw; sepals colored; buds acute; fruits on gynophores 1–3 mm long. ..... 2. *Streptanthus.*
s. Petals white or lavender, less than 1 cm long, not crisped, often gradually attenuate to a clawlike base; sepals greenish; buds obtuse; fruits sessile or nearly so. ..32. *Arabis.*
p. Fruits terete or quadrangular, very rarely slightly flattened; petals commonly yellow, sometimes white or lavender.
t. Leaves entire, cordate-amplexicaul; mature fruits strongly quadrangular; seeds readily releasing abundant mucilage when wet. .....13. *Conringia.*

t. Leaves (at least some of them) pinnately lobed or petiolate; fruits terete or obscurely 4-angled; seeds not mucilaginous (very rarely producing a thin coat of mucilage) when wet.
u. Valves of fruits nerveless or obscurely nerved; seeds biseriately or rarely uniseriately arranged; plants aquatic or of very wet habitats.
v. Flowers yellow; median nectaries present outside the inner stamens; leaves simple, sinuate or pinnately lobed; lower nodes usually lacking adventitious roots. . . . . 35. *Rorippa.*
v. Flowers white or lavender; median nectaries lacking; leaves pinnate; lower nodes with adventitious roots. . . . . 34. *Nasturtium.*
u. Valves with a prominent midnerve; seeds uniseriately arranged; plants mostly terrestrial.
w. Lower leaves cordate or reniform, dentate, not auriculate; seeds longitudinally striate. . . . . 40. *Alliaria.*
w. Lower leaves pinnate and/or auriculate; seeds reticulate.
x. Flowers white or lavender; inflorescence an elongated raceme; cauline leaves serrate or entire, cuneate. . . . . 29. *Iodanthus.*
x. Flowers yellow; inflorescence corymbose; cauline leaves pinnately lobed, the uppermost sometimes unlobed.
y. Valves 3-nerved; fruits terete; cotyledons incumbent; cauline leaves not auriculate. . . . . 41. *Sisymbrium.*
y. Valves 1-nerved; fruits slightly flattened or somewhat 4-angled; cotyledons accumbent; cauline leaves auriculate or amplexicaul. . . 28. *Barbarea.*

Full treatments of the tribes, including references, distributions, and aspects of their biology, will appear in separate papers as in the sequence below. The following brief accounts for the tribes are mainly intended to provide guidelines for the tribal limits and for the number of representative species and genera in the southeastern United States.

Tribe 1. **Thelypodieae** Prantl in Engler & Prantl, Nat. Pflanzenfam. III. **2:** 155. 1891.

Herbaceous annuals or biennials, rarely perennials, glabrous or with simple hairs only; sepals equal at base or sometimes slightly saccate, erect or spreading to reflexed, occasionally forming an urceolate or bilabiate calyx; petals often strongly differentiated into claw and blade, usually crisped or channeled; stamens exserted or slightly protruding, equal in length or somewhat tetradynamous, rarely in 3 unequal pairs, not appendaged; siliques dehiscent, linear, several to many times longer than broad, terete or flattened parallel to the septum, often borne on a distinct gynophore; seeds winged or wingless, not mucilaginous when wet; cotyledons accumbent or incumbent. (Including Stanleyeae Robinson, Romanschulzieae O. E. Schulz, Streptantheae O. E. Schulz.)
TYPE GENUS: *Thelypodium* Endl.

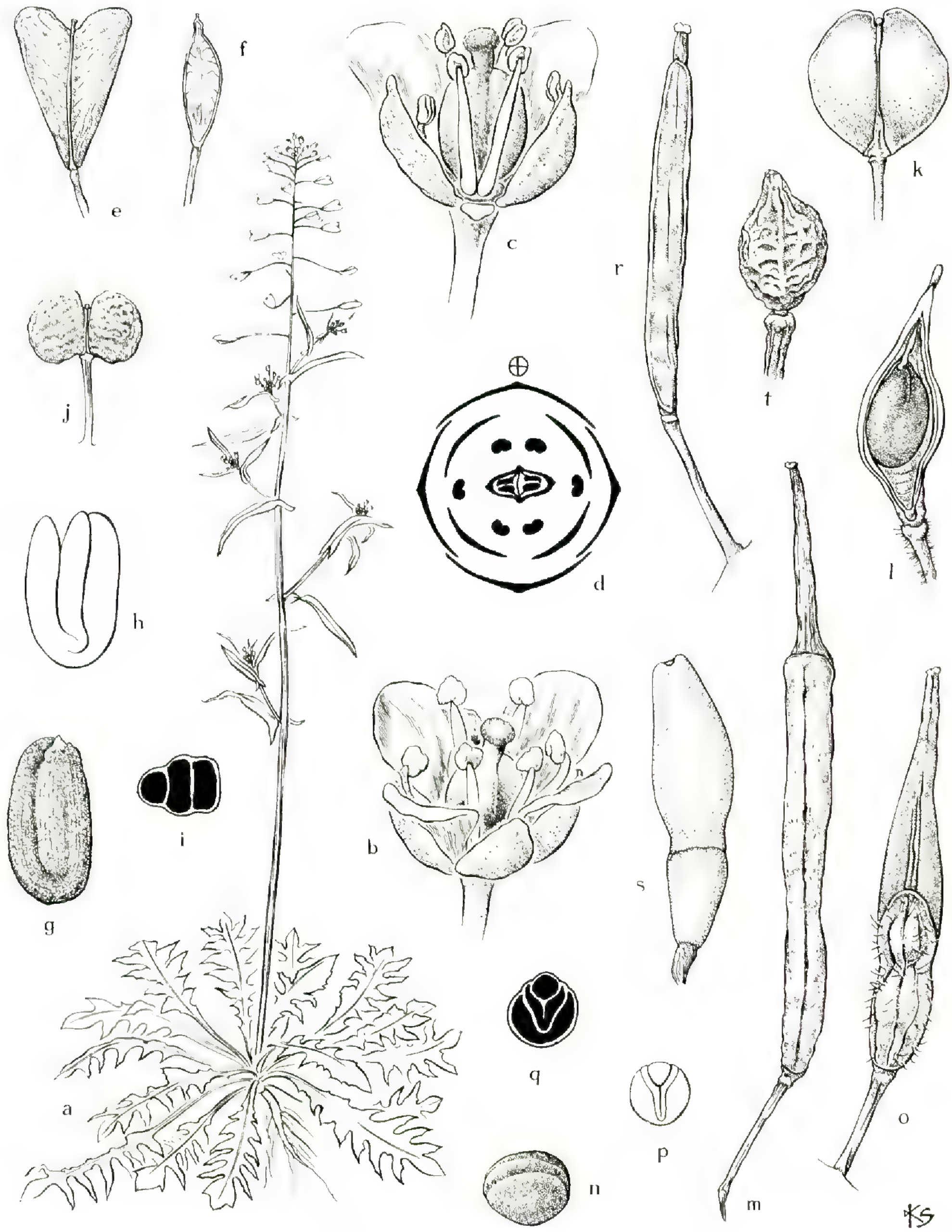

FIGURE 1. Tribes **Lepidieae** and **Brassiceae.** a–l, LEPIDIEAE. a–i, *Capsella bursa-pastoris:* a, plant with flowers and fruits, × ½; b, flower, × 12; c, flower with sepal and two petals removed, × 12; d, floral diagram; e, fruit, × 3; f, replum and septum, × 3; g, seed, × 25; h, embryo, oriented as in seed, × 25; i, diagrammatic cross section of seed showing incumbent cotyledons, × 25. j, *Coronopus didymus,* fruit, × 6. k, *Lepidium virginicum,* fruit, × 6. l, *L. campestre,* fruit after removal of valve—note apical attachment of seed, × 6. m–t, BRASSICEAE. m, n, *Brassica campestris:* m, fruit, × 2; n, seed, × 6. o–q, *Sinapis alba:* o, fruit, × 2; p, embryo, × 6; q, diagrammatic cross section of seed showing conduplicate cotyledons, × 6. r, *Diplotaxis muralis,* fruit, × 3. s, *Cakile edentula* subsp. *Harperi,* fruit—note transverse joint, × 1½. t, *Calepina irregularis,* fruit, × 6.

A natural tribe of 11 genera and some 110 species; represented in our area by seven indigenous species in two genera, *Warea* Nutt. and *Streptanthus* Nutt.

Tribe 2. **Brassiceae** DC. Syst. Nat. **2:** 152. 1821.

Annual, biennial, or perennial herbs, sometimes subshrubs or large shrubs, glabrous or with simple hairs only; sepals erect or spreading, often saccate at base; petals usually clawed; stamens tetradynamous, the filaments very rarely appendaged; siliques long or short, dehiscent or indehiscent, often clearly differentiated into valvular and stylar (beak) segments, 1 or both seed-bearing, or the fruits transversely jointed or lomentaceous and breaking into parts, terete, angular, or flattened; seeds mucilaginous or not when wet, winged or wingless; cotyledons almost always conduplicate (very rarely accumbent or incumbent). (Including Cakilineae DC., Calepineae Godron, Erucarieae DC., Psychineae DC., Raphaneae DC., Velleae DC., Zilleae DC.) TYPE GENUS: *Brassica* L.

A natural tribe of some 52 genera and about 230 species; represented in the Southeast by 21 species, all (except four of *Cakile* Miller) naturalized weeds belonging to 11 genera: *Brassica, Erucastrum* Presl, *Hutera* Porta, *Sinapis* L., *Diplotaxis* DC., *Eruca* Miller, *Raphanus* L., *Rapistrum* Crantz, *Cakile, Calepina* Adanson, and *Conringia* Heister ex Fabr.

Tribe 3. **Lepidieae** DC. Syst. Nat. **2:** 151. 1821.

Annual, biennial, or perennial herbs, sometimes subshrubs or shrubs, glabrous or usually pubescent with simple hairs only; sepals erect or spreading, rarely conspicuously saccate at base; petals often slightly differentiated into blade and claw; stamens 6, tetradynamous, or reduced to 4 or 2, the filaments frequently appendaged; siliques almost always shorter than 3 times their width, dehiscent or indehiscent, occasionally didymous and schizocarpic, always compressed at right angles to the septum (angustiseptate), replum much narrower than width of the fruit; seeds often mucilaginous when wet, winged or wingless; cotyledons accumbent or incumbent. (Including Brachycarpeae DC., Iberideae Godron, Isatideae DC., Senebiereae Godron, Subularieae DC., Thlaspideae DC.) TYPE GENUS: *Lepidium* L.

A natural tribe of over 60 genera and more than 600 species; represented in our area by *Lepidium, Coronopus* Zinn, *Cardaria* Desv., *Thlaspi* L., *Teesdalia* R. Br., and *Capsella* Medicus, and about 16 species, of which all (except four species of *Lepidium*) are introduced weeds.

Tribe 4. **Alysseae** Godron in Gren. & Godron, Fl. France **1:** 112. 1848.

Herbaceous annuals, biennials, or perennials, rarely subshrubs or shrubs, usually with branched or stellate trichomes, sometimes the trichomes simple or absent; sepals erect or spreading; petals attenuate at base or occasionally strongly clawed; stamens 6, tetradynamous, rarely 4, often with appendaged, toothed, or winged filaments, infrequently slender at base; siliques almost always shorter than 3 times their width, dehiscent or rarely indehiscent, spherical,

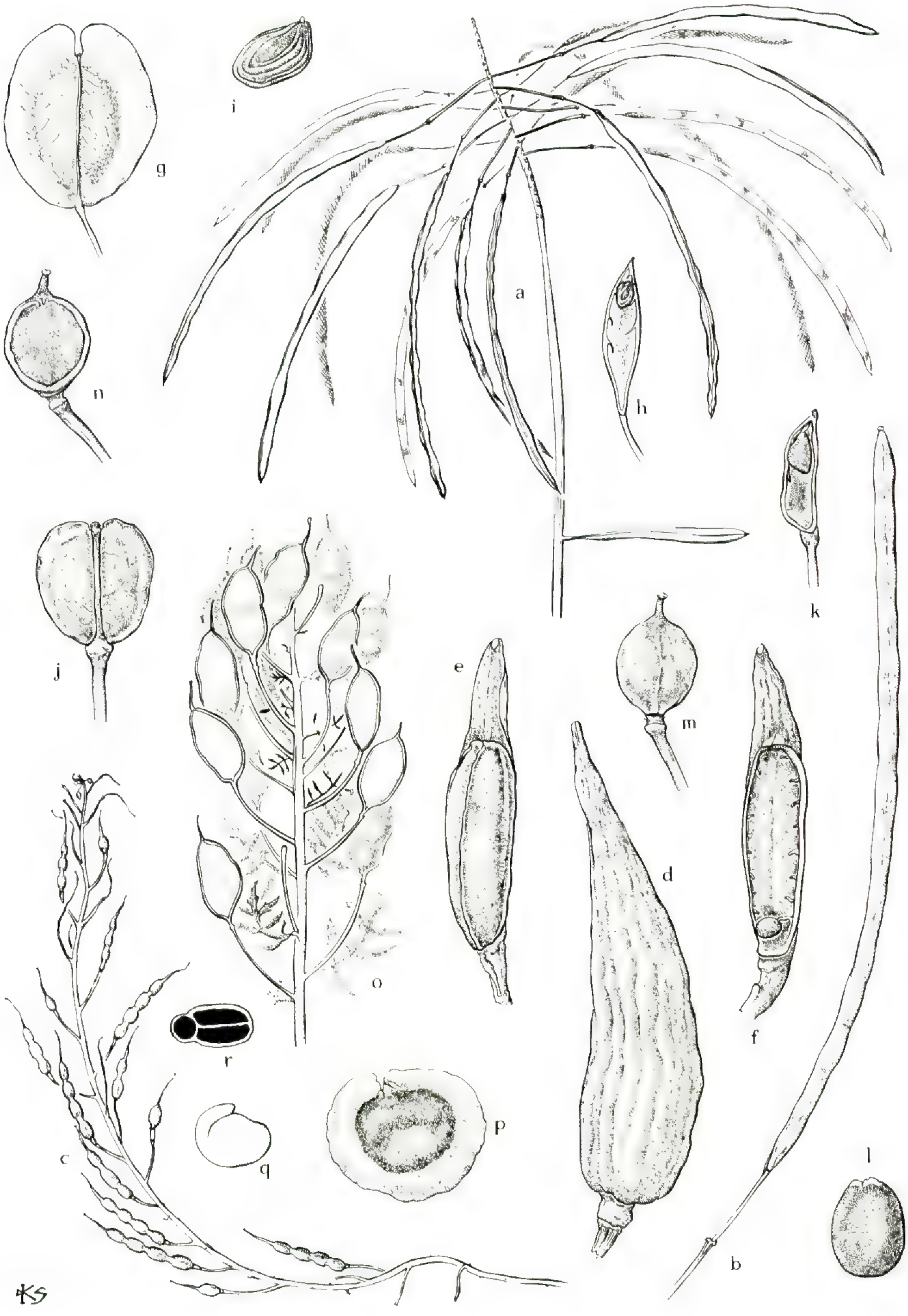

FIGURE 2. Tribes **Thelypodieae, Brassiceae, Lepidieae, Alysseae,** and **Arabideae.** a, b, THELYPODIEAE, *Warea Carteri:* a, infructescence, × 1; b, fruit—note gynophore, × 2. c–f, BRASSICEAE. c, *Raphanus Raphanistrum,* infructescence—note lomentaceous fruits, × ½. d, *R. sativus,* fruit—note aborted lower segment, × 2. e, f, *Eruca vesicaria* subsp. *sativa:* e, fruit—note beak, × 2; f, fruit after fall of valves. g–l, LEPIDIEAE. g–i, *Thlaspi arvense:* g, fruit, × 2; h, fruit after fall of valves, × 2; i, seed, × 6. j–l, *Teesdalia nudi-*

inflated, or commonly compressed parallel to the septum (latiseptate); seeds mucilaginous or not when wet, winged or wingless; cotyledons accumbent, very rarely incumbent. (Including Camelineae DC., Drabeae O. E. Schulz, Lunarieae O. E. Schulz, Physarieae Robinson.) TYPE GENUS: *Alyssum* L.

A tribe with poorly defined boundaries and comprising a heterogeneous assemblage of 41 genera and some 750 species; represented in our area by 20 species (13 indigenous) and seven genera: *Lunaria* L., *Alyssum, Lobularia* Desv., *Berteroa* DC., *Draba* L., *Lesquerella* S. Watson, and *Camelina* Crantz.

Tribe 5. **Arabideae** DC. Syst. Nat. **2:** 161. 1821.

Annual, biennial, or perennial herbs, rarely subshrubs, glabrous or with simple, furcate, or branched hairs; sepals often ascending or spreading, equal or saccate at base; stamens tetradynamous, with slender or very rarely toothed filament bases; stigmas entire or slightly 2-lobed; siliques dehiscent, narrowly linear, sometimes oblong, rarely subspherical, often compressed parallel to the septum, occasionally inflated; seeds winged, margined, or sometimes wingless; cotyledons accumbent. (Including Cardamineae Calestani.) TYPE GENUS: *Arabis* L.

A tribe with a natural core of large genera and their relatives (but with artificially drawn boundaries) consisting of more than 570 species in 36 genera; represented in the Southeast by 44 species, of which only nine are introduced weeds, and ten genera: *Cardamine* L., *Barbarea* R. Br., *Iodanthus* Torrey & Gray ex Steudel, *Leavenworthia* Torrey, *Selenia* Nutt., *Arabis, Sibara* Greene, *Nasturtium* R. Br., *Rorippa* Scop., and *Armoracia* Gaertner, Meyer, & Scherb.

Tribe 6. **Hesperideae** Prantl in Engler & Prantl, Nat. Pflanzenfam. III. **2**: 154. 1891.

Annual, biennial, or perennial herbs, rarely subshrubs or shrubs, glabrous or with simple, bifurcate, branched, or stellate trichomes, occasionally with multicellular glands; sepals erect, sometimes connivent; petals usually differentiated into blade and claw; stamens tetradynamous, filaments of the median pairs usually expanded at base or connate; stigma 2-lobed or very rarely entire, the lobes commonly decurrent; siliques long or short, dehiscent or rarely indehiscent, occasionally lomentaceous, infrequently beaked or appendaged; seeds often wingless; cotyledons incumbent or accumbent. (Including Anchonieae DC., Cheirantheae Villani, Erysimeae Reichenb., Matthioleae O. E. Schulz, Schizopetaleae R. Br. ex Barn.) TYPE GENUS: *Hesperis* L.

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caulis: j, fruit, × 6; k, fruit after fall of valves, × 6; l, seed, × 12. m, n, ALYSSEAE, *Lobularia maritima:* m, fruit, × 6; n, replum and septum, × 6. o–r, ARABIDEAE, *Selenia aurea:* o, infructescence—note bracts, × 1; p, seed—note wing, × 6; q, embryo, × 6; r, diagrammatic cross section of seed showing accumbent cotyledons, × 6.

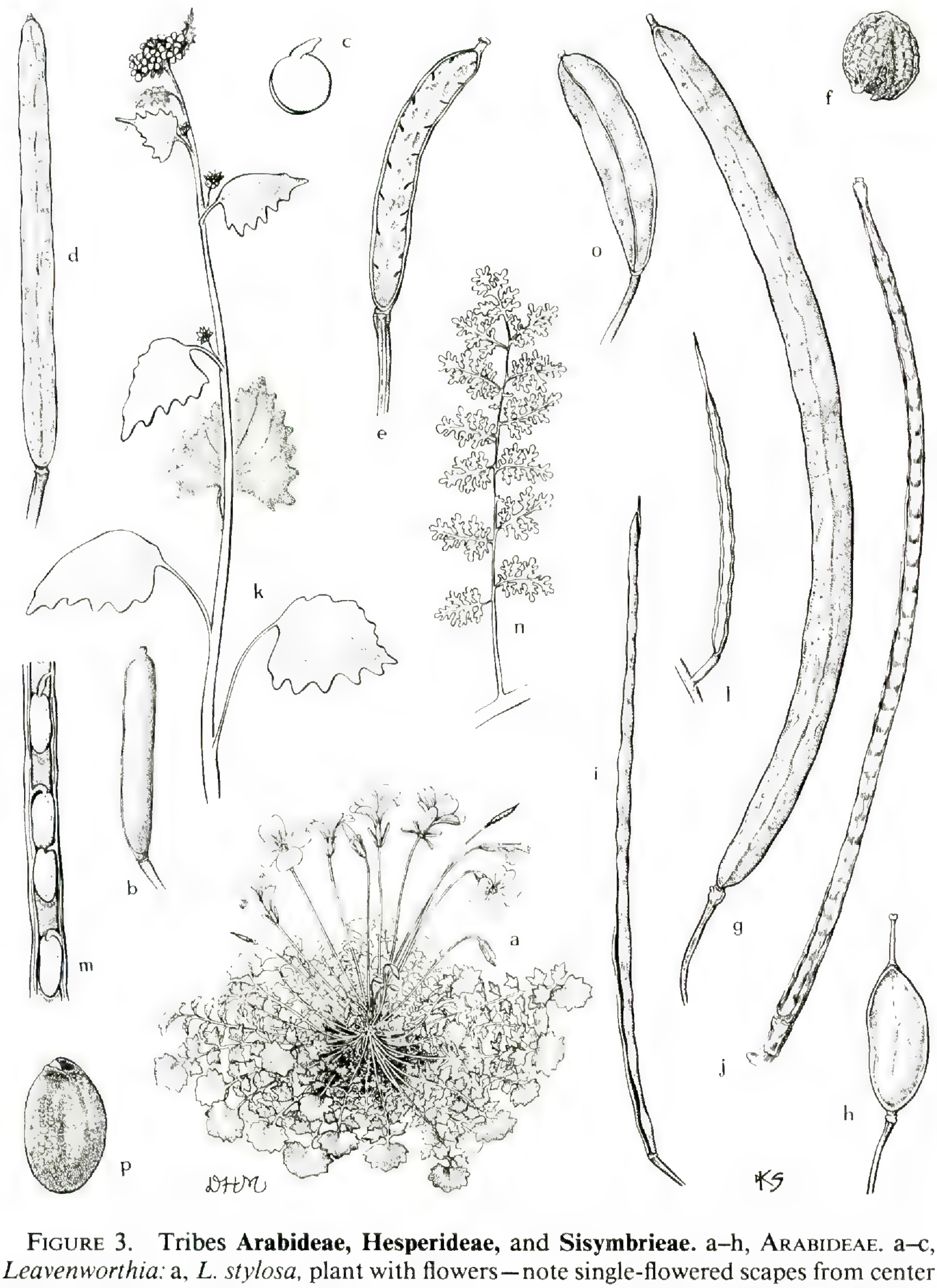

FIGURE 3. Tribes **Arabideae, Hesperideae,** and **Sisymbrieae.** a–h, ARABIDEAE. a–c, *Leavenworthia:* a, *L. stylosa,* plant with flowers—note single-flowered scapes from center of basal rosette, × ½; b, *L. uniflora,* fruit, × 1; c, *L. torulosa,* embryo—note straight radicle, × 6. d, *Sibara virginica,* fruit, × 3. e, f, *Nasturtium officinale:* e, replum and septum—note funiculi of biseriately arranged seeds, × 3; f, seed, × 12. g, *Arabis canadensis,* fruit, × 2. h, *Armoracia aquatica,* fruit, × 3. i, j, HESPERIDEAE: i, *Hesperis matronalis,* fruit, × 1; j, *Erysimum repandum,* fruit, × 2. k–p, SISYMBRIEAE. k–m, *Alliaria petiolata:* k, portion of plant with flowers, × ½; l, fruit, × 1; m, portion of fruit after removal of valve—note uniseriate arrangement of seeds, × 3. n–p, *Descurainia pinnata:* n, tripinnatisect leaf, × ½; o, fruit, × 6; p, seed, × 25.

A tribe with a fairly natural core of genera (but with highly artificial boundaries) consisting of some 43 genera and about 500 species; represented in our area by six species in the genera *Chorispora* R. Br. ex DC., *Hesperis,* and *Erysimum* L.

Tribe 7. **Sisymbrieae** DC. Syst. Nat. **2:** 150. 1821.

Annual, biennial, or perennial herbs, rarely shrubs, glabrous or with simple, furcate, or dendritic trichomes; sepals ascending or spreading; petals differentiated or not into claw and blade; stamens tetradynamous, the filaments linear and usually neither appendaged nor toothed; stigma entire or 2-lobed; siliques usually much longer than broad, dehiscent or rarely indehiscent; generally terete or inflated; seeds primarily wingless, mucilaginous or not when wet; cotyledons incumbent. TYPE GENUS: *Sisymbrium* L.

A highly artificial tribe with some 70 genera and about 400 species; represented in our area by seven species (one indigenous) in four genera: *Alliaria* Scop., *Sisymbrium, Arabidopsis* Heynh., and *Descurainia* Webb & Berth.

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INFLORESCENCE ARCHITECTURE AND EVOLUTION IN THE FAGACEAE

ROBERT B. KAUL AND ERNST C. ABBE

INFLORESCENCE ARCHITECTURE is receiving increasing attention with respect to its role in the life of plants, but much remains to be learned of its effects on pollination and dispersal biology (see Wyatt, 1982). Little is known of the biology of fagaceous inflorescences or of their relationships with the growth or the reproductive patterns of the trees. Most studies (Abbe, 1974; Macdonald, 1979; Fey & Endress, 1983) have concentrated on the nature of the flower clusters (often called dichasia or partial inflorescences) and cupules. Hjelmqvist (1948) and Soepadmo (1972) briefly reviewed the variety of inflorescences in the Fagaceae. Čelakovský (1889) compared fagaceous inflorescences with betulaceous and juglandaceous ones and enumerated the criteria by which he judged levels of specialization. Jäger (1980) analyzed inflorescences of the Betulaceae, the family perhaps closest to the Fagaceae. For this study, we have analyzed a sample of Fagaceae much larger than those of previous workers, and we here assess their inflorescences in terms of structural as well as functional criteria. Although our emphasis is on Paleotropical species, some species of the northern Temperate Zone are also included. The APPENDIX lists the species studied, as well as the provenance of the specimens.

The family Fagaceae comprises perhaps 900 species. It is most richly represented in eastern and southeastern Asia and the nearby islands of the western Pacific Ocean. In many places the family dominates the forests, and on a worldwide basis it is perhaps second in biomass only to the conifers (Soepadmo, 1972; Heywood, 1978).

In tropical areas the Fagaceae are found from sea level to the frost line, but they are most abundant and often dominant at middle altitudes, where they favor rain forests of little seasonality. There the trees are evergreen and bear mostly entire to slightly sinuate or dentate leaves that sometimes have drip-tips. At higher latitudes in the Northern Hemisphere, the Fagaceae occur in both ever-wet and seasonally dry climates, where they are evergreen or deciduous and their leaves are entire to sharply dentate or deeply lobed. The Southern-Hemisphere genus *Nothofagus* grows in cool montane forests and is mostly evergreen.

Castanea has about ten species in mesic forests of the eastern and southeastern United States, eastern Asia, southern Europe, northern Africa, and the Middle East. All are deciduous. The closely related *Castanopsis* has perhaps 120 species

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in eastern and southeastern Asia and western-Pacific islands; there is a single species, *C. chrysophylla,* in montane forests of North America from Washington to California.

Lithocarpus (ca. 300 species) occurs from India to Japan, New Guinea, and Java. It, too, has a single North American representative, *L. densiflora,* in California and southwestern Oregon.

Quercus (ca. 450 species) is widespread and often abundant across all the northern continents, as well as North Africa, at low and middle latitudes. It extends south in the Andean cordillera to about the equator. In Central America, from the Isthmus of Tehuantepec to Colombia, there are 46 species (C. H. Muller, 1942), but in southeastern Asia, from Thailand to Java and Borneo, there are only 19 (Soepadmo, 1972).

Trigonobalanus has three species: *T. verticillata* Forman in southeastern Asia, southern China (Yunnan), and a few islands of the East Indies; *T. daichangensis* (A. Camus) Forman in Thailand; and *T. excelsa* Lozano, Hernández, & Henao in Colombia.

Forman (1964) and Soepadmo (1972) recognized three subfamilies: Castaneoideae (*Castanea, Castanopsis, Lithocarpus* s.l.), Quercoideae (*Quercus* s.l., *Trigonobalanus*), and Fagoideae (*Fagus, Nothofagus*). Crepet and Daghlian (1980) supported the close affinity of *Quercus* and *Trigonobalanus,* but Lozano and colleagues (1979) placed *Trigonobalanus* alone in Trigonobalanoideae. Kuprianova (1963) suggested that *Nothofagus* constitutes its own family, Nothofagaceae; Nixon (1982) concurred and also suggested betulacean affinities for it.

Asiatic and western-Pacific Fagaceae have been variously interpreted at the species level by Camus (1929, 1934–1954), Barnett (1942, 1944), and Soepadmo (1968, 1970, 1972). The most recent monograph (Soepadmo, 1972) is based on extensive field and herbarium work.

Generic circumscription is complicated in *Castanea, Castanopsis, Lithocarpus,* and *Quercus* by intermediate characters variously shared among them. *Trigonobalanus* is distinctive. Soepadmo (1972) has acknowledged the essential unity of *Castanea* and *Castanopsis,* the former differing from the latter only in having pistillate flowers always at the base of the spikes and bearing six or more stigmas. He rejected Hjelmqvist's (1948) proposal of generic status (*Chrysolepis*) for the single species of western North American *Castanopsis,* but Forman (1966), Abbe (1974), and others have accepted it. Forman (1964), Soepadmo (1972), and Abbe (1974) recognized *Quercus* as distinct from *Lithocarpus,* despite historical confusion. They noted the constancy of differences including unisexual inflorescences, with the staminate ones pendent (*Quercus*), vs. bisexual erect inflorescences (*Lithocarpus*). There are floral differences as well.

The distinctions between *Lithocarpus* and *Castanopsis* are usually obvious; except for a few species, the genera can be distinguished by the structure of their cupules (Forman, 1966; Soepadmo, 1972).

The affinities of *Fagus* to the other genera—and even to *Nothofagus*—are less certain. In recent decades there has been no confusion concerning the identity of *Fagus* such as there has been about *Castanea, Castanopsis, Litho-*

carpus, and *Quercus.* These latter four genera form a coherent unit and, with *Trigonobalanus,* are the topic of this paper.

Pollination in Fagaceae is by insects or wind. *Castanea, Castanopsis, Lithocarpus,* and *Trigonobalanus verticillata* are entomophilous, have scented flowers, and bear erect staminate inflorescences. *Castanea* and *Castanopsis* attract clouds of dipterans and other insects with their heavy, almost unpleasant odor; *Lithocarpus* is more delicately scented. *Trigonobalanus daichangensis* has pendulous staminate catkins and is anemophilous (Hjelmqvist, 1948; Soepadmo, 1972), as are *Quercus, Fagus,* and *Nothofagus.* Reports of entomophily in *Quercus* (e.g., Faegri & Van der Pijl, 1979) are perhaps based on species of *Lithocarpus* placed in synonymy with *Quercus. Trigonobalanus excelsa,* recently discovered in Colombia (Lozano *et al.,* 1979), is possibly entomophilous because it too has more or less erect staminate inflorescences. Except for the studies of entomophily in *Castanea* by Porsch (1950), Clapper (1954), and Jaynes (1974), there seem to be no definitive assessments of entomophily in the Fagaceae, however. The possibility that some entomophilous species are partially anemophilous (see Proctor & Yeo, 1972; Faegri & Van der Pijl, 1979) should be explored.

Anemophily was present in the family by the Middle Eocene (Crepet, 1979) and was probably a factor leading to its prominence—especially that of *Quercus*—in north-temperate forests (Endress, 1977). Fossils from the Middle Eocene show floral structures almost identical to those of modern Castaneoideae (Crepet & Daghlian, 1980). Thus, the family was well advanced by the Middle Eocene and, in fact, is known from the Campanian and Santonian stages of the Cretaceous (J. Muller, 1981).

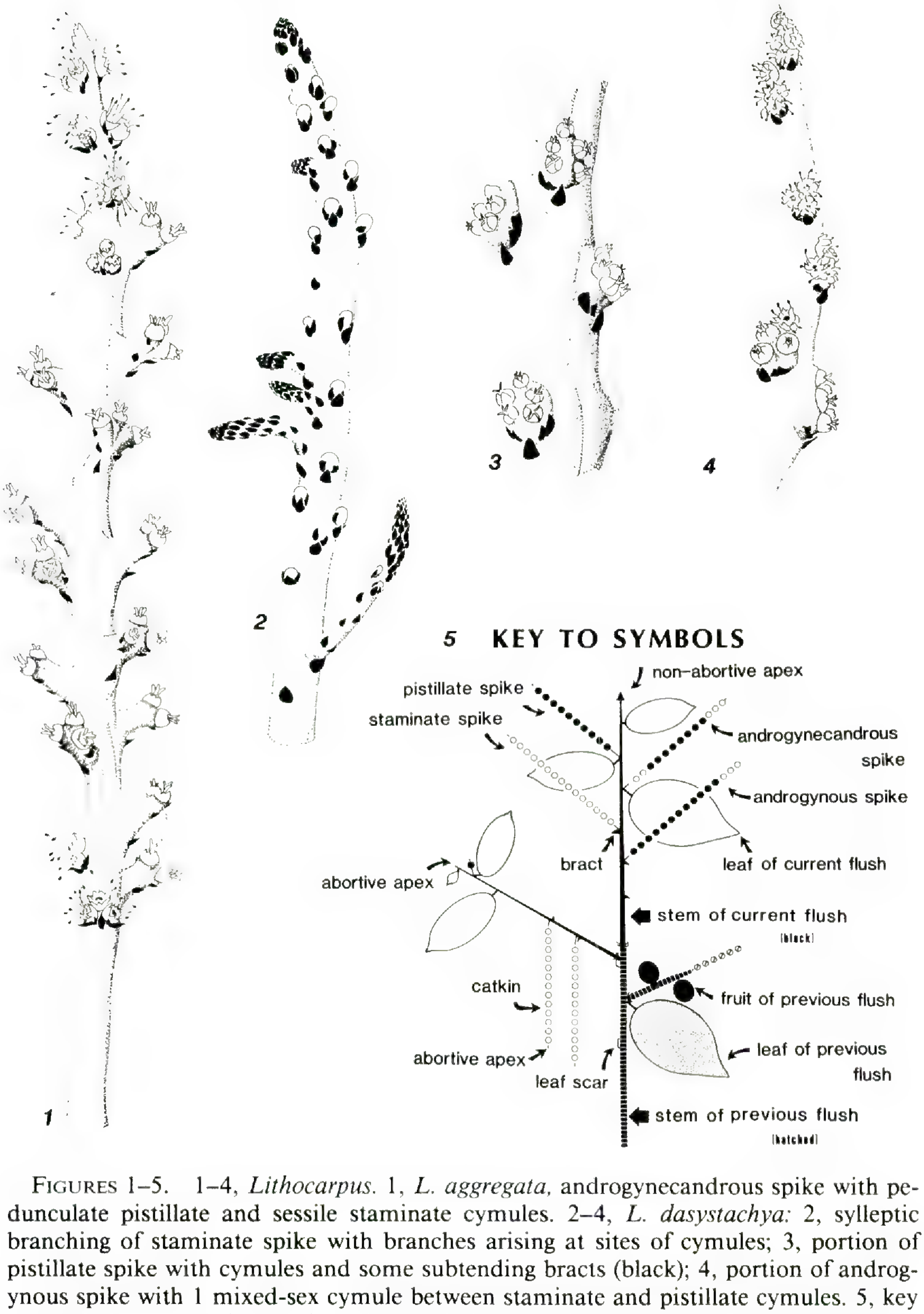
The Fagaceae originated from unknown ancestors that were probably shared with Betulaceae and perhaps other families, but details are unclear. However, the Fagaceae form a large enough group—and one with enough diversity of inflorescence structure—to provide useful internal comparisons that suggest probable evolutionary pathways.

MATERIALS AND METHODS

We examined 126 species in *Castanea, Castanopsis, Lithocarpus, Quercus,* and *Trigonobalanus,* including thousands of specimens from our collections of Asiatic and western-Pacific Fagaceae as well as a few critical North American and European species. We and our colleagues collected in Paleotropical and eastern Asian forests, and for some species we have multiple collections from certain individual trees over a year's time. Most of our Paleotropical specimens have been annotated by Soepadmo, and the nomenclature herein follows his treatment (Soepadmo, 1972).

Each illustration represents an actual specimen at or near anthesis. Because the Fagaceae are so variable, no single figure can depict all the variance in a species or even on an individual tree. For illustration we have chosen species and individuals that best show the diversity of structure.

Where possible, each figure shows current and previous flushes of growth. When leaves from the previous flush were present, as they often were (most



FIGURES 1–5. 1–4, *Lithocarpus.* 1, *L. aggregata,* androgynecandrous spike with pedunculate pistillate and sessile staminate cymules. 2–4, *L. dasystachya:* 2, sylleptic branching of staminate spike with branches arising at sites of cymules; 3, portion of pistillate spike with cymules and some subtending bracts (black); 4, portion of androgynous spike with 1 mixed-sex cymule between staminate and pistillate cymules. 5, key to symbols used in illustrations (open circles, staminate cymules; blackened circles, pistillate cymules).

tropical and many temperate species are evergreen), they are shown shaded (see FIGURE 5). New leaves of the current flush are unshaded, and their relative sizes are approximated. However, because the new leaves continue to expand

after anthesis, many of them would ultimately be relatively larger than shown. No attempt is made to indicate actual leaf shapes or sizes.

Because of the very large number of small flowers in each inflorescence, it is not possible to show individual flowers in these diagrams. Therefore, staminate and pistillate cymules are indicated with open and blackened circles, respectively. The relative lengths of the rows of circles suggest only the relative lengths of the floriferous axes, not the actual numbers of flowers. In most cases the number of staminate cymules and flowers is much larger (sometimes by factors of hundreds) than the number of open circles.

DEFINITIONS

There are no standard, universal definitions for inflorescences like those existing for flowers, and it is unlikely that such definitions are possible. Rather, each group requires careful review of both the applicable inflorescence terminology and the accompanying definitions. Even the term "inflorescence" cannot be applied equivalently in all angiosperm taxa. Definitions applied at the level of flowering plants may be descriptively useful but often produce little evolutionary information.

In the Fagaceae, as in other angiosperms and especially in trees and shrubs, delimitation of inflorescences is not always obvious and no terminology exists that adequately covers all configurations. We use *total inflorescence* for all the synchronously produced floriferous axes on a *shoot system,* whether or not they are aggregated into a defined "synflorescence" (Troll, 1964) or "conflorescence" (Briggs & Johnson, 1979). A *shoot system* is here intended to mean a major indeterminate axis that clearly has a *leader* and reproductive branches bearing *spikes* or *catkins* (erect or pendent floriferous axes, respectively). The total inflorescence can include branches produced by nonresting buds of the current flush (*sylleptic* branches), those produced by axillary buds of the previous flush (*proleptic* branches), or both.

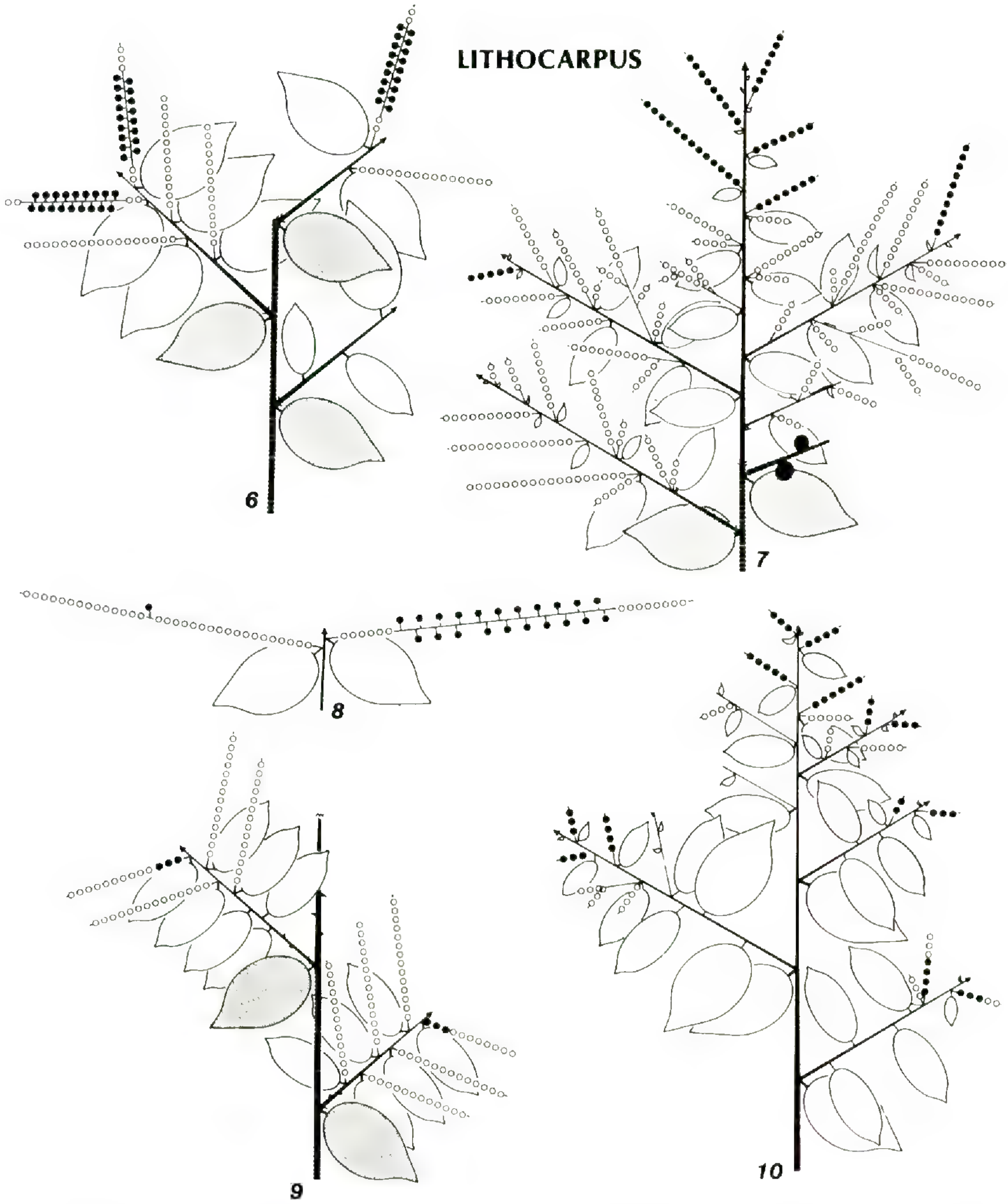
No axis (including spikes and catkins) that we examined in this study terminated in an abortive or functional floral bud. In the parlance of Briggs and Johnson (1979), all of these axes are blastotelic (terminate in a nonfloral bud); some are auxotelic (producing continuing growth with or without a dormant period; *indeterminate*), while others are anauxotelic (not continuing growth; *determinate*). Spikes and catkins are determinate, as are some vegetative branches; the leader and some vegetative branches are indeterminate.

Bract refers to any nonfoliar leaf homologue in any branch order. *Foliose* defines an axis bearing only normal foliage leaves, while *folio-bracteose* indicates axes with both bracts and leaves. *Bracteose* axes bear only bracts at the nodes.

OBSERVATIONS

Distribution of Flowers on Spikes and Catkins

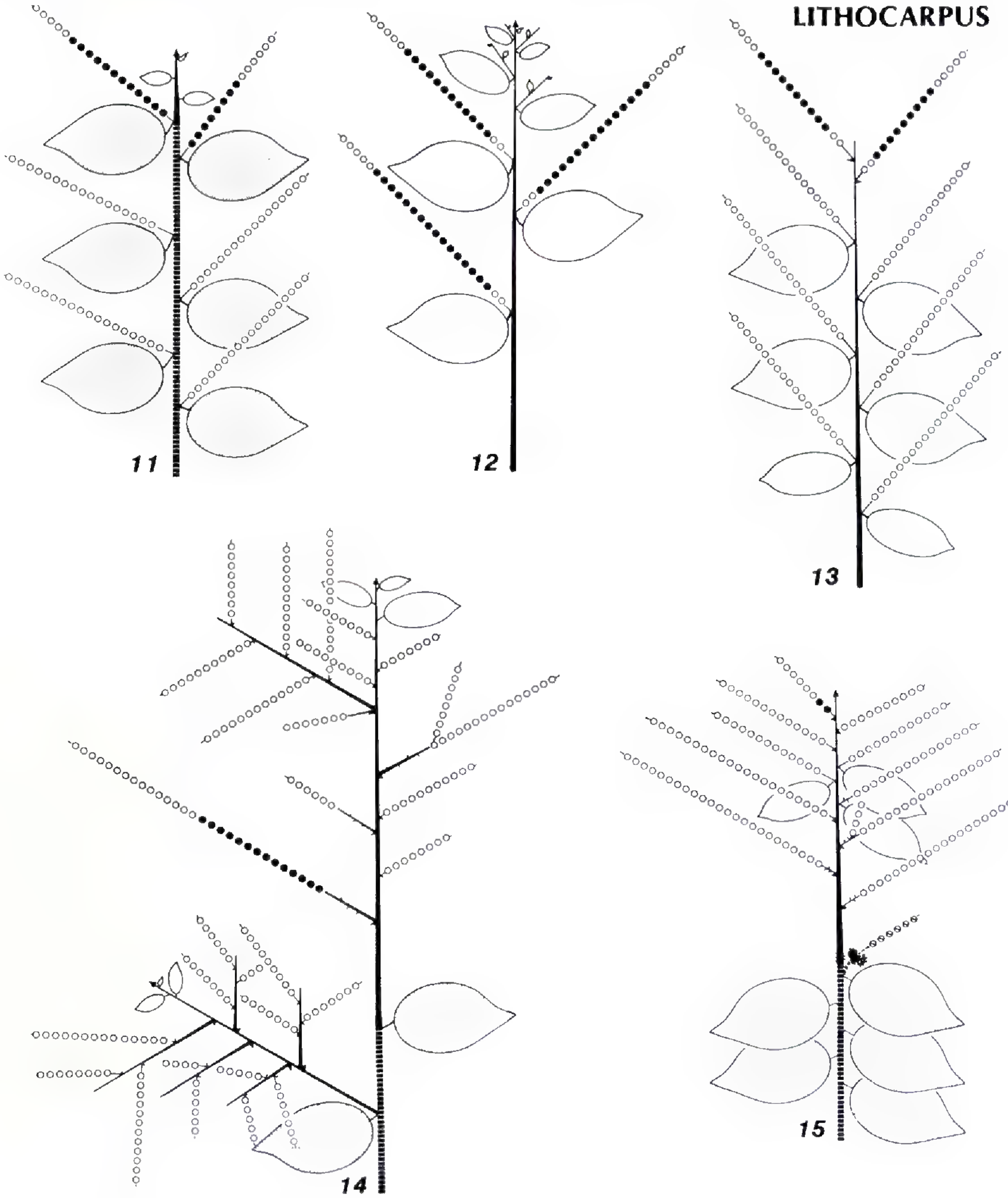
Flowers are always arranged singly or in groups of 2 to 25 or more along the axis of a spike or catkin. Although the groups of florets are often called "di-



FIGURES 6–10. *Lithocarpus:* 6, *L. aggregata,* with distinctly pedunculate pistillate cymules; 7, *L. nodosa,* with sylleptic and proleptic branching; 8, *L. sootepensis,* with pedunculate pistillate cymules; 9, *L. amygdalifolia*; 10, *L. havilandii,* showing sylleptic branching.

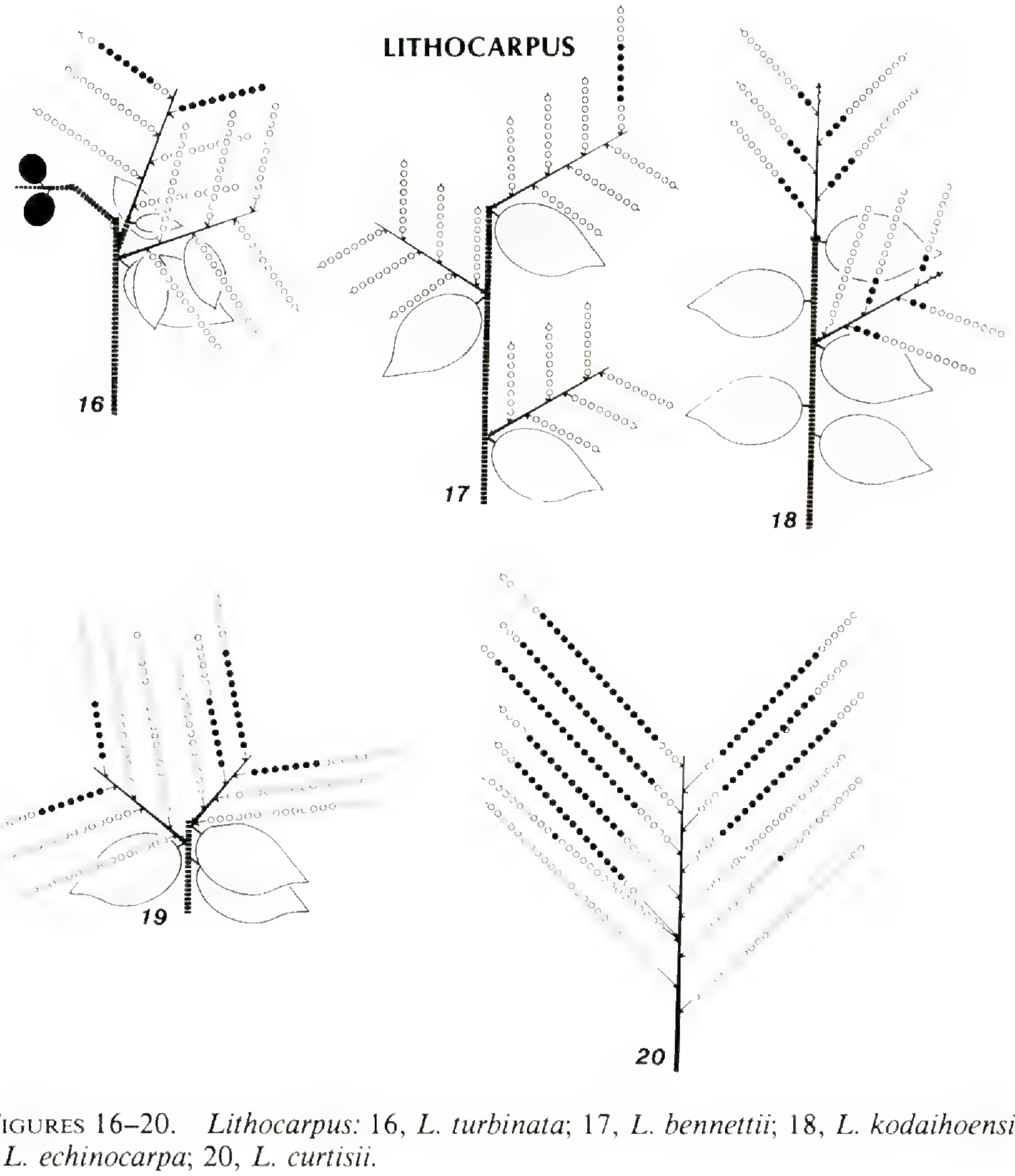
chasia" in the literature, they are sometimes monochasial. Less specific terms are "cymule" and "partial inflorescence." The details are often obscure because of miniaturization and cupule development, and the diverse theories concerning the basic character of the cupule necessitate caution in the assignment of a specific branching pattern to the cymules (see Fey & Endress, 1983). The cymules are short-shoots on the elongate axis of the spike or catkin, which is a long-shoot.

Spikes are entirely staminate, entirely pistillate, androgynous (with the sta-



FIGURES 11–15. *Lithocarpus:* 11, *L. ewyckii,* with proleptic axillary spikes synchronous with beginnings of new shoot growth; 12, *L. bolovensis,* with sylleptic androgynecandrous spikes; 13, *L. thomsonii*; 14, *L. cooperta*; 15, *L. densiflora,* with 1 branched staminate spike.

minate cymules distal to the pistillate—see, for example, FIGURES 5, 11), gynecandrous (with the pistillate cymules in the distal position—e.g., FIGURE 27), or androgynecandrous (with the pistillate cymules between groups of staminate ones—e.g., FIGURES 5, 6). Occasionally staminate and pistillate cymules are mixed or parallel along short segments of the spikes. Perfect flowers and mixed-sex cymules (FIGURE 4) are common and often occur at the boundary between staminate and pistillate segments of a spike. Catkins, which occur only in *Quercus* (FIGURES 39, 44–66) and *Trigonobalanus daichangensis* (FIGURE 69), are always staminate.



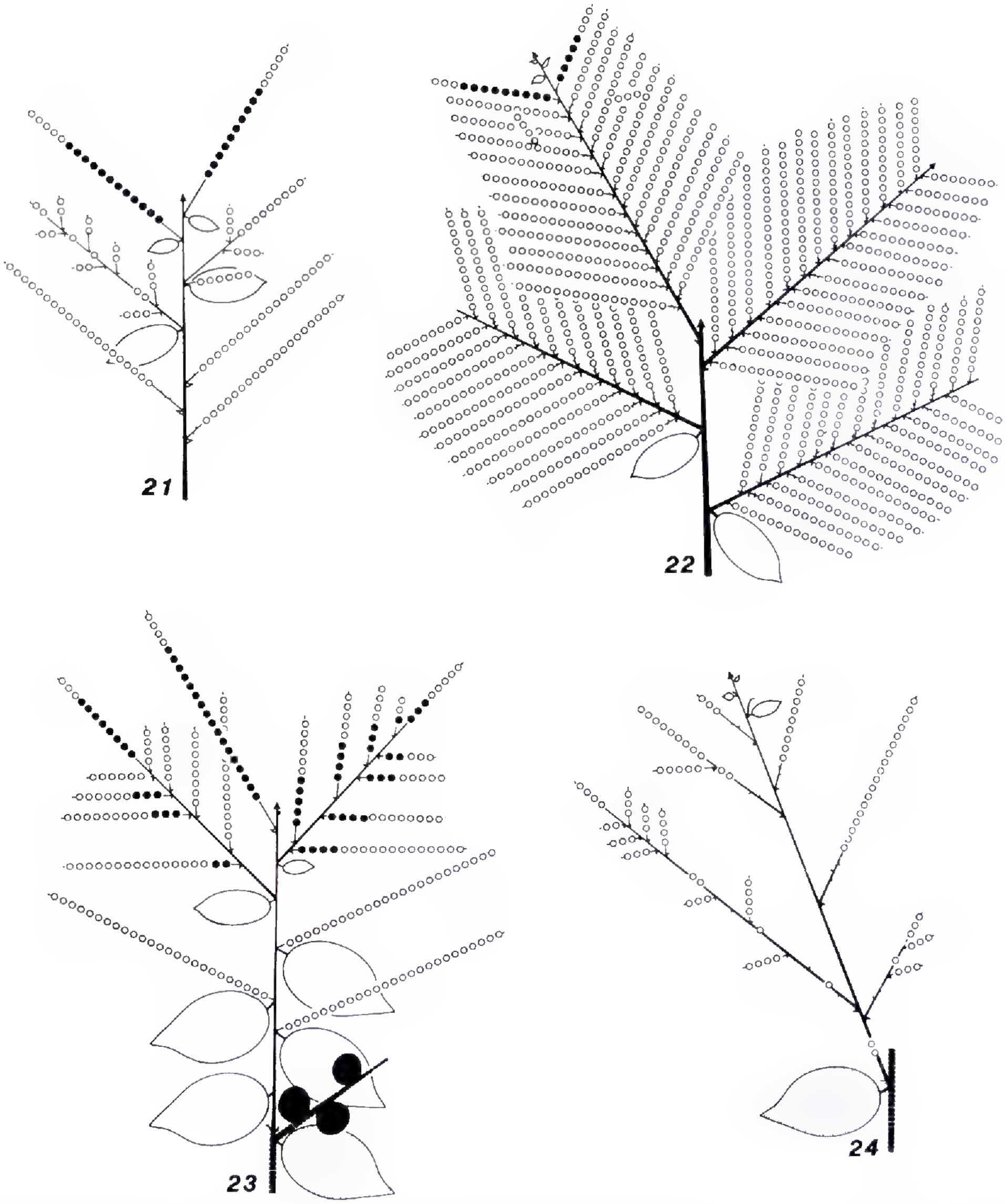
FIGURES 16–20. *Lithocarpus:* 16, *L. turbinata*; 17, *L. bennettii*; 18, *L. kodaihoensis*; 19, *L. echinocarpa*; 20, *L. curtisii*.

Each cymule is subtended by one or more bracts (FIGURES 1–4), but these are not illustrated in FIGURES 5–70.

GROWTH PATTERNS AND THE DISTRIBUTION OF SPIKES AND CATKINS

Tropical Fagaceae often have several flushes a year, most of them floriferous but not always synchronous on a tree or among conspecifics of an area. Northern Fagaceae are usually presumed to have a single flush, but we observed as many as five in five species of *Quercus* during a wet summer in Nebraska. In these the flushes were separated by one- to three-week intervals, and only the first of the season was floriferous; proleptic branches occurred in all but the final flush.

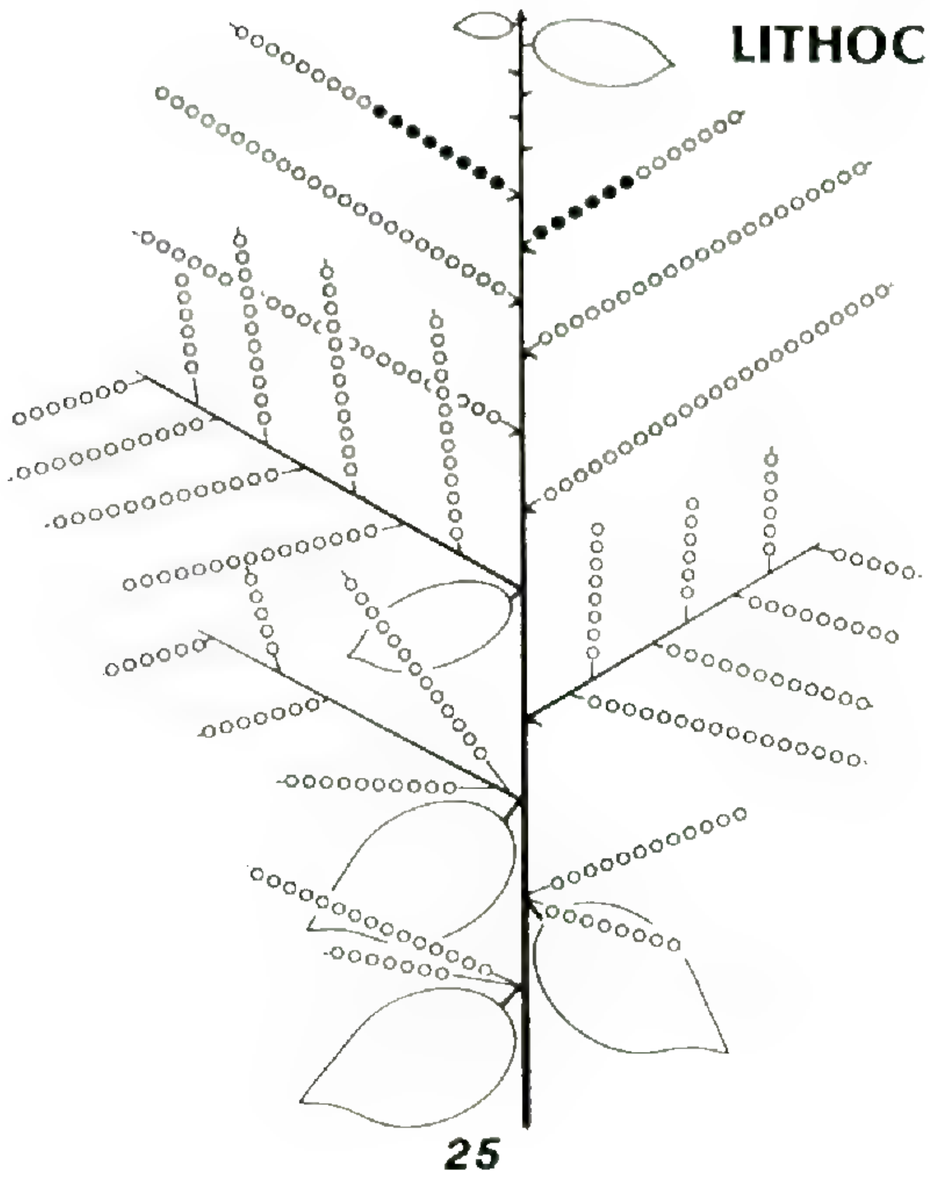
Shoots, leaves, spikes, and catkins are produced synchronously. Extension growth is monopodial from terminal buds of the previous flush. Dormant lateral buds of the previous flush also can produce proleptic extension growth, inflo-

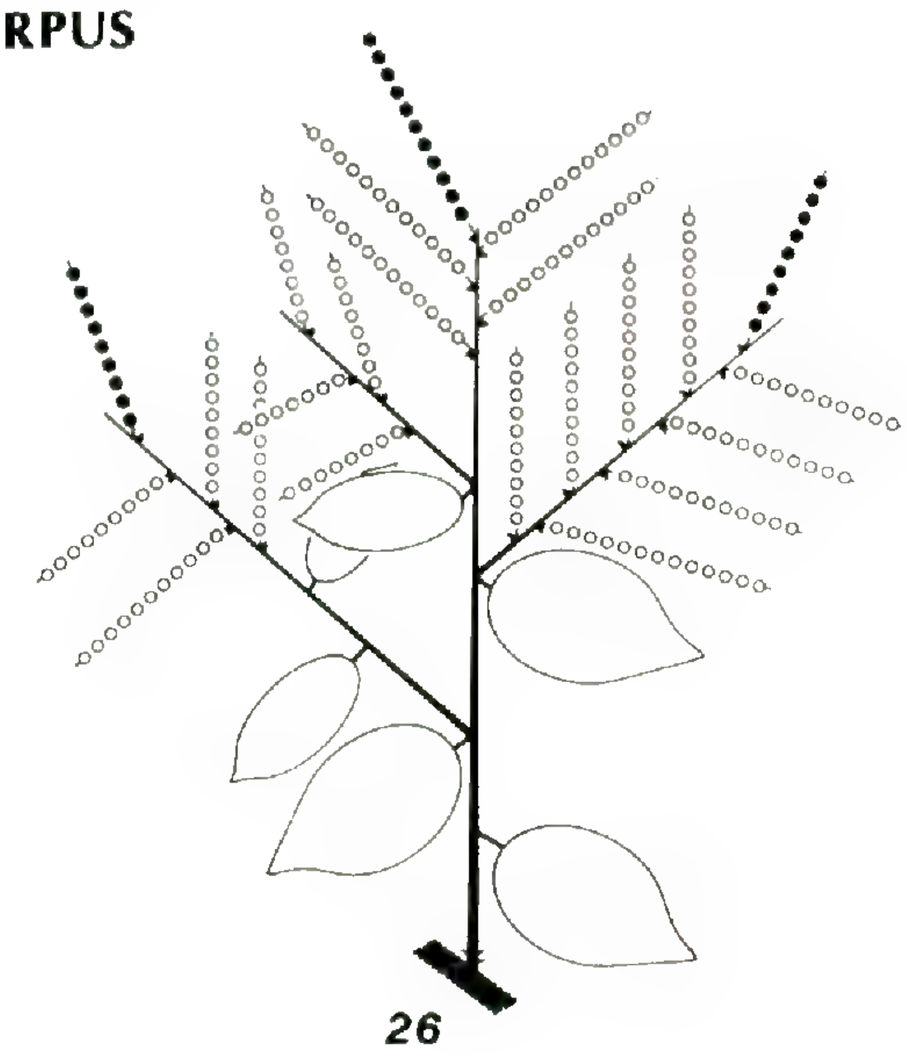


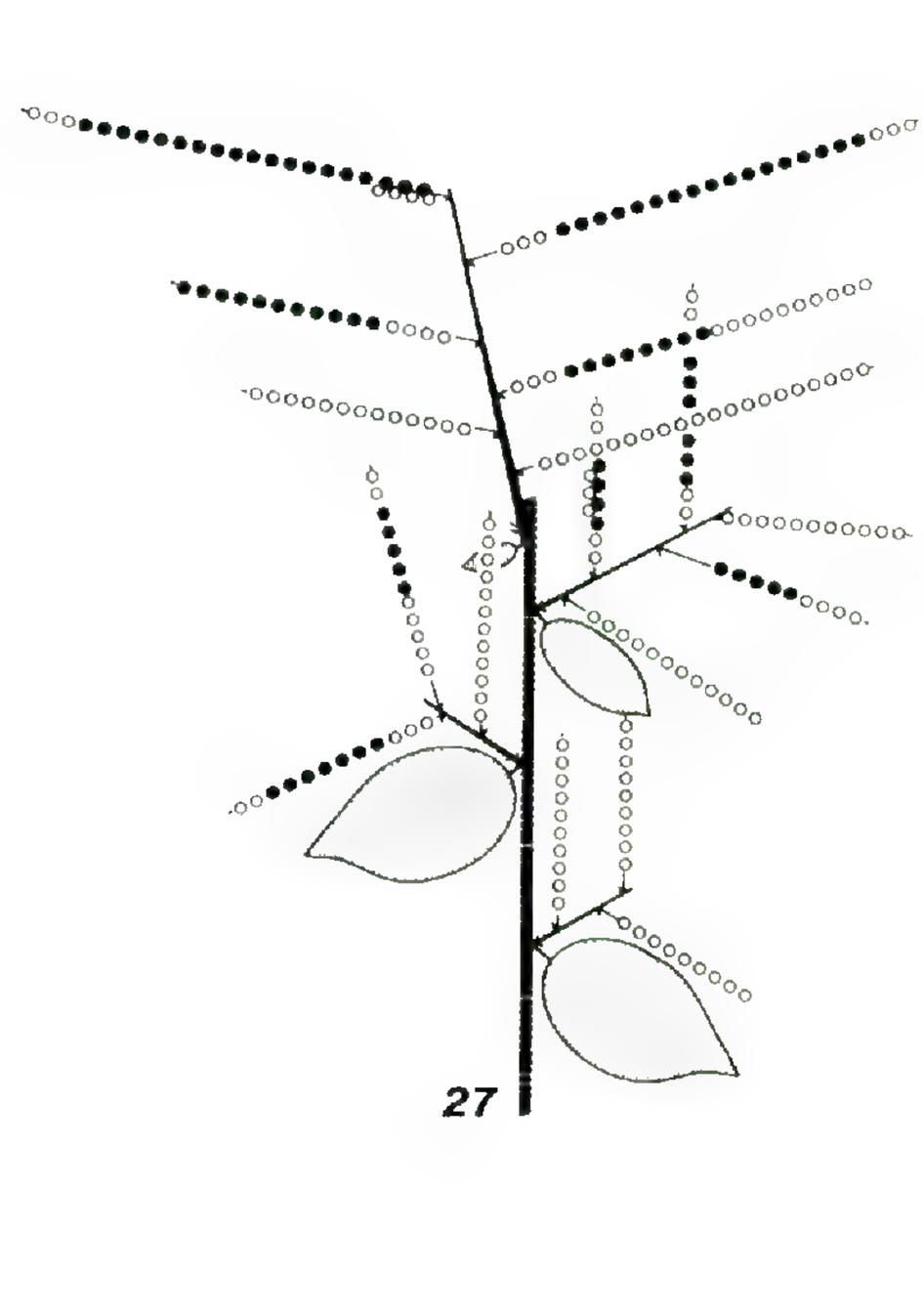
FIGURES 21–24. *Lithocarpus.* 21, 22, *L. sundaica:* specimen with 2 branched staminate spikes; 22, specimen with 4 large reproductive branches, the distal 2 indeterminate, the uppermost 1 with few weakly branched staminate spikes and some pistillate dichasia. 23, *L. lampadaria,* with 2 branched bisexual spikes. 24, *L. cooperta,* with 3 branched staminate spikes.

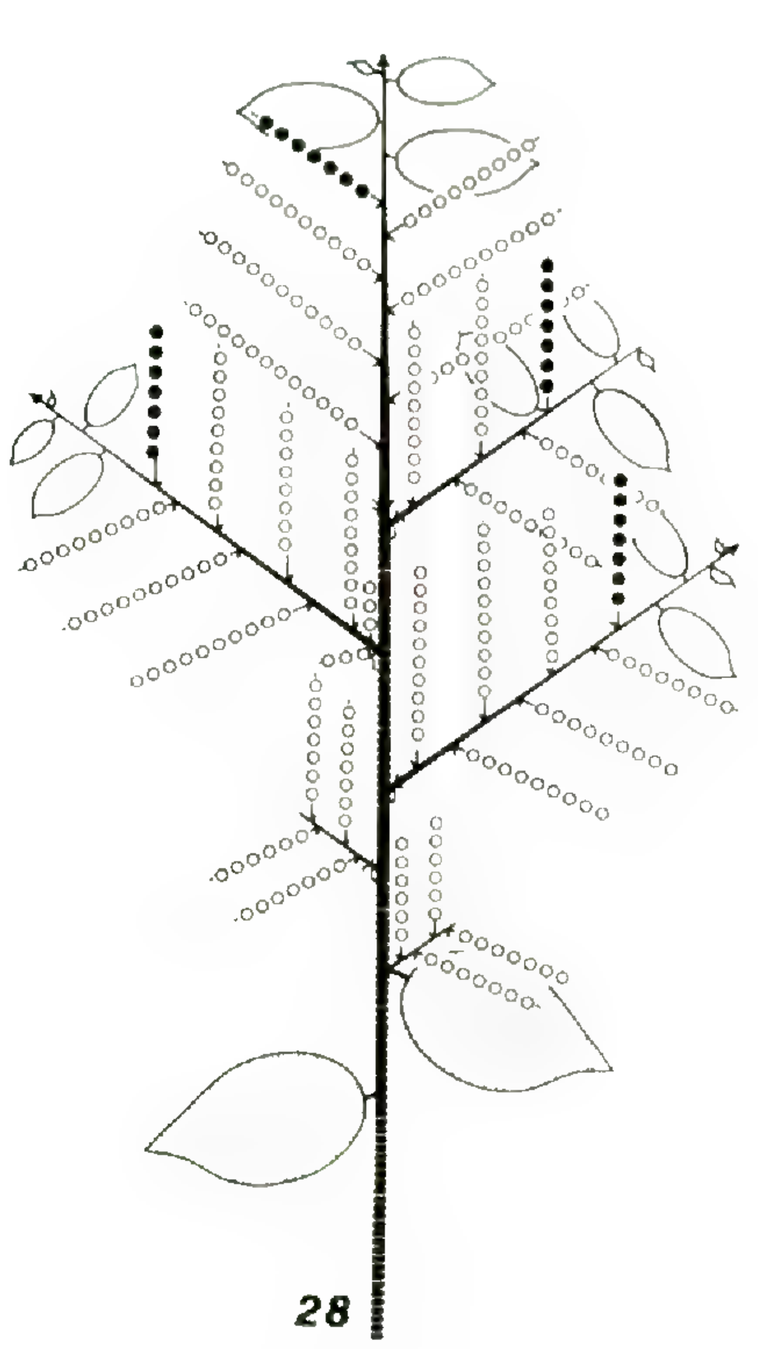
rescences, or both. The growth of many, if not all, species of *Castanea, Castanopsis, Lithocarpus,* and *Quercus* conforms to Rauh's model (see Hallé *et al.,* 1978), in which the rhythmic monopodial growth pattern of the trunk is repeated in the branches. *Trigonobalanus verticillata* conforms to Attim's model (Hallé *et al.,* 1978), which resembles Rauh's model except that growth is continuous (nonrhythmic).

Nearly every leaf has a spike or reproductive branch in its axil at some time,







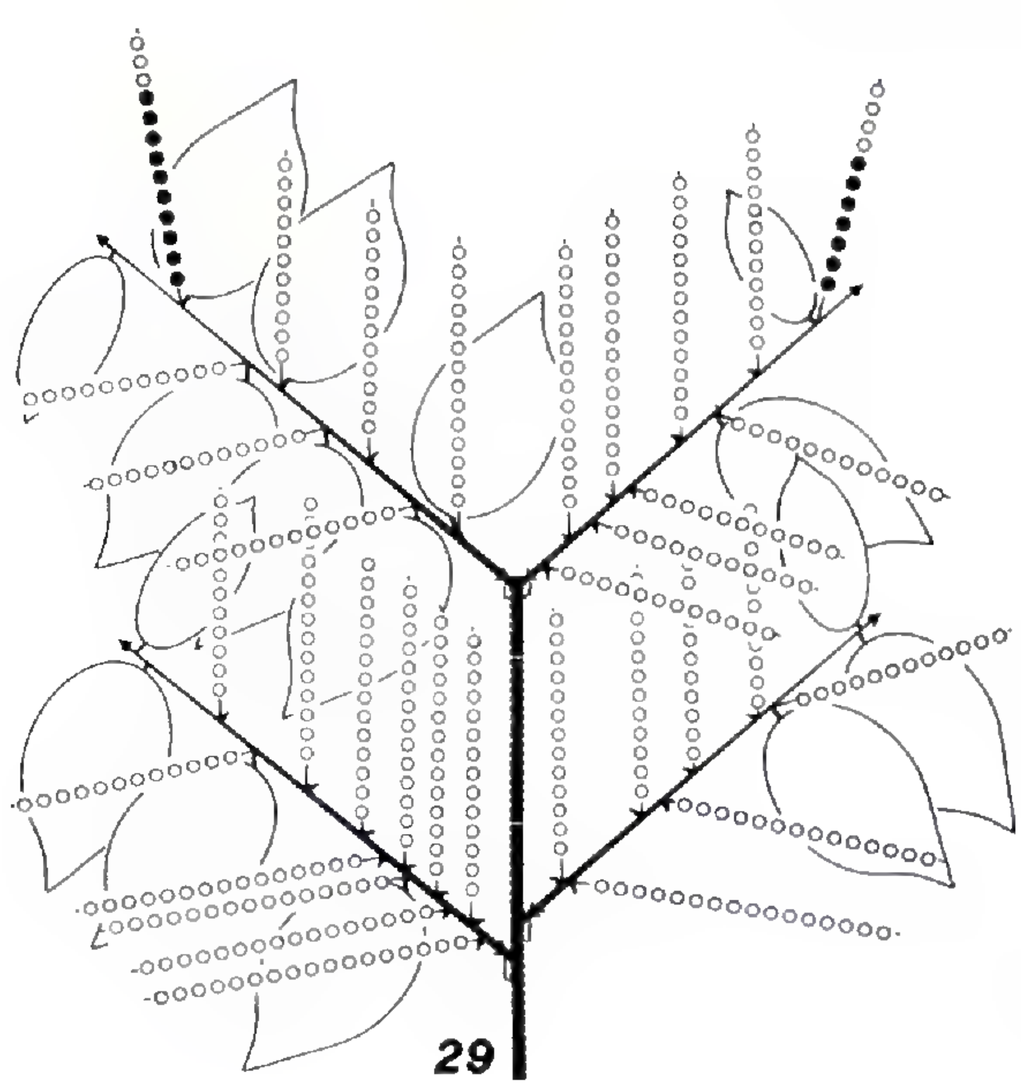


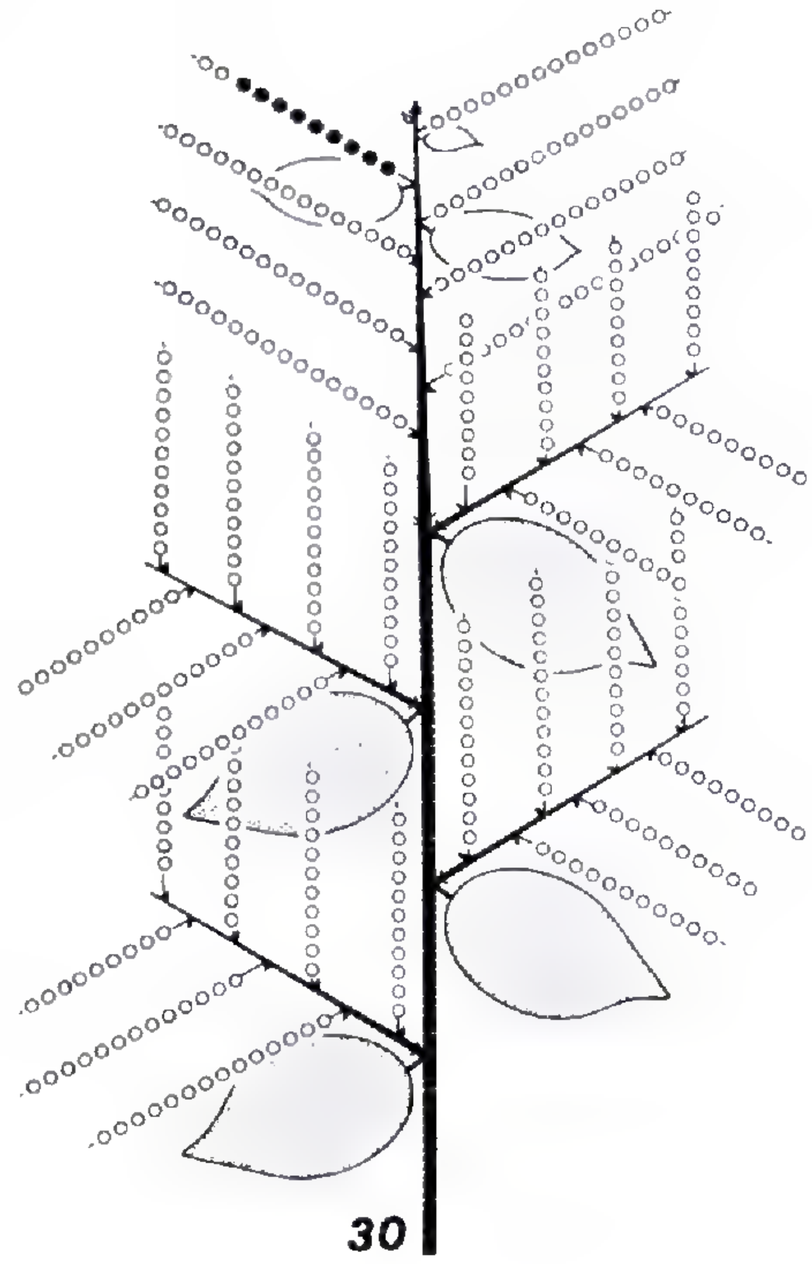
FIGURES 25–28. *Lithocarpus:* 25, *L. nieuwenhuisii*; 26, *L. caudatifolia*; 27, *L. curtisii*; 28, *L. kawakamii*.

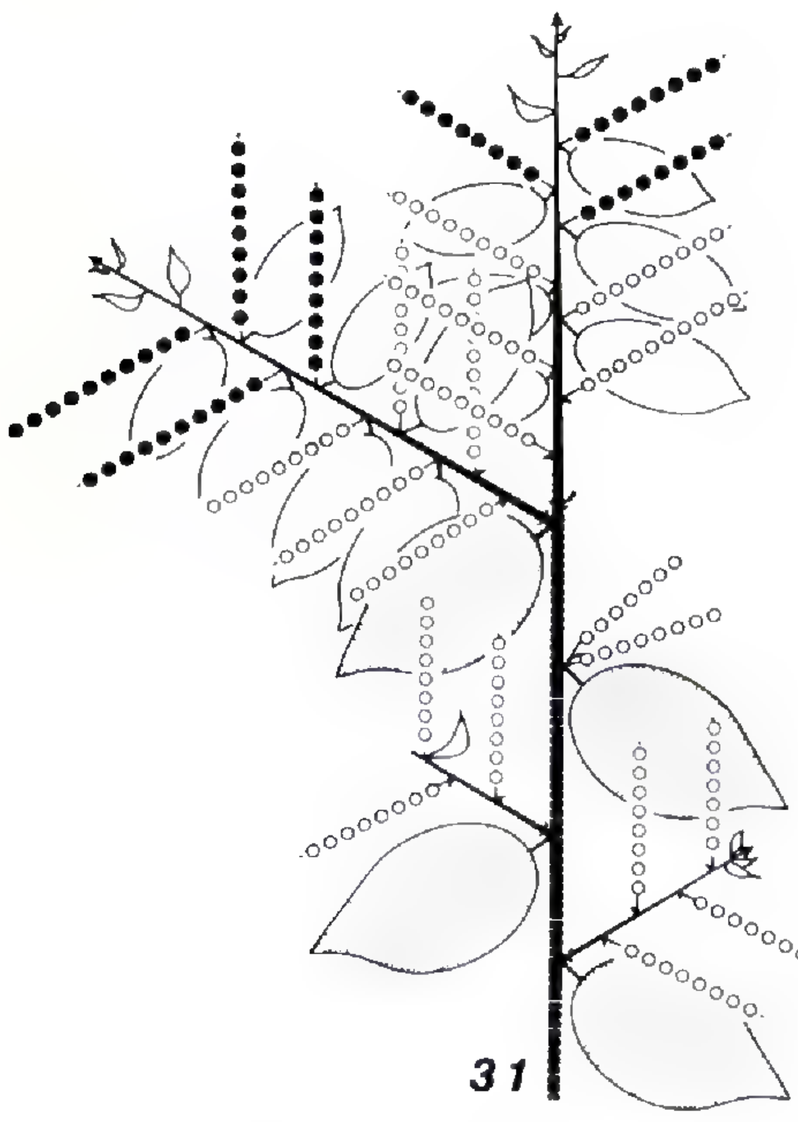
and in that sense most of the tree is once part of an inflorescence. In some species the foliage leaves subtend individual spikes (e.g., FIGURES 11–13, 36, 40–45). The leader and most foliose branches are indeterminate. Indeterminate folio-bracteose branches are distally foliose and proximally bracteose (e.g., FIGURES 29, 35, 39).

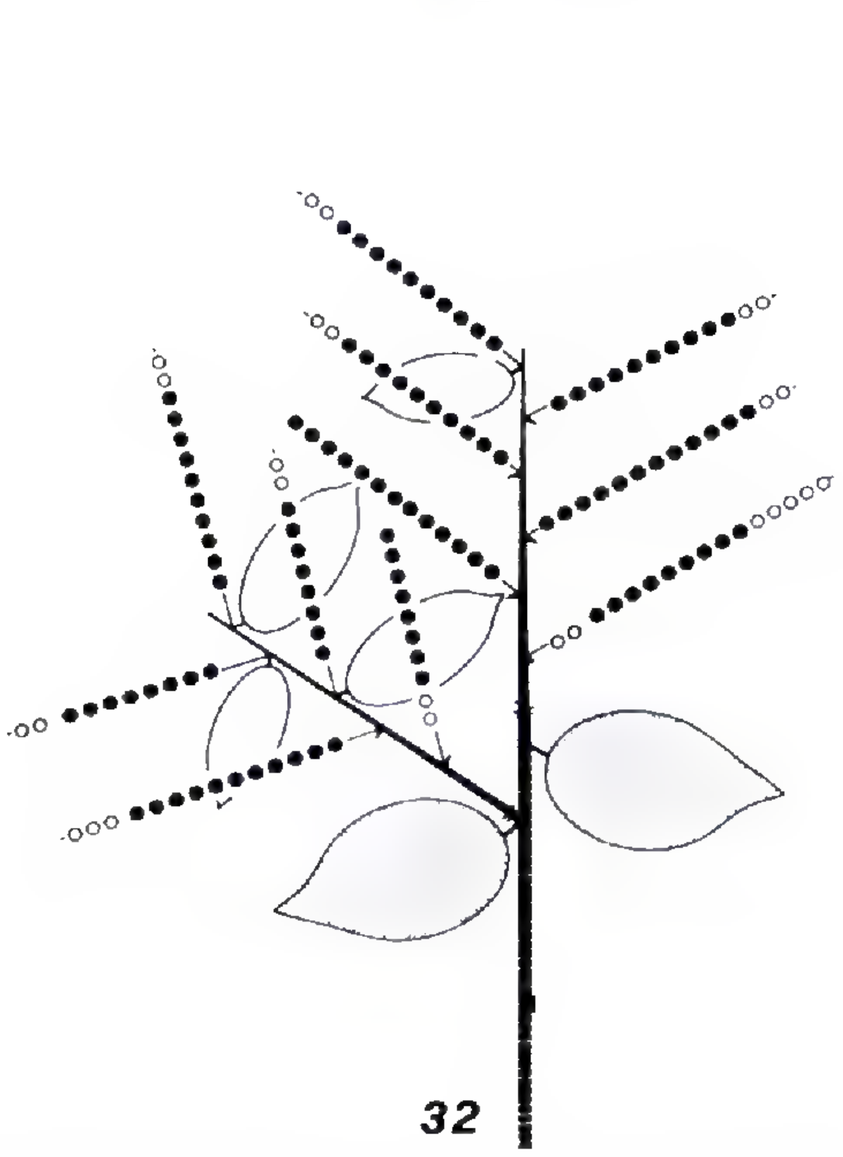
Bracteose reproductive branches are often determinate (e.g., FIGURES 14, 16–18). Those bearing staminate spikes and catkins are shed soon after anthesis,

CASTANOPSIS





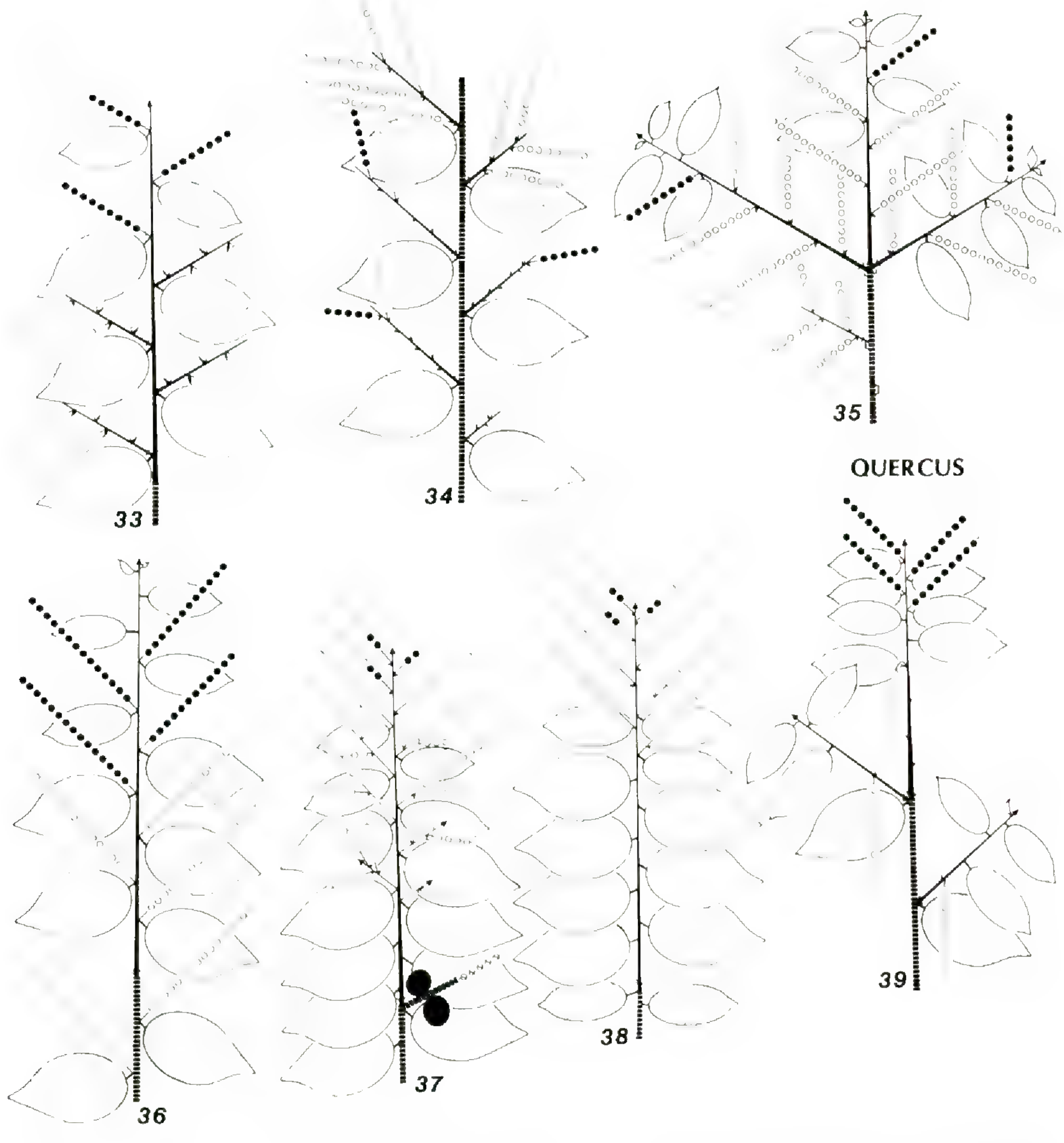




FIGURES 29–32. *Castanopsis:* 29, *C. inermis*; 30, *C. fissa*; 31, *C. acuminatissima*; 32, *C. rhamnifolia.*

while those with pollinated pistillate flowers are retained but usually drop their staminate spikes or flowers. These determinate branches are sometimes present on the same axis with indeterminate ones (e.g., FIGURES 22, 28, 31), in which case they are usually proximal and the indeterminate branches distal on the axis. Furthermore, they are often smaller than the distal branches and bear fewer spikes with fewer flowers.

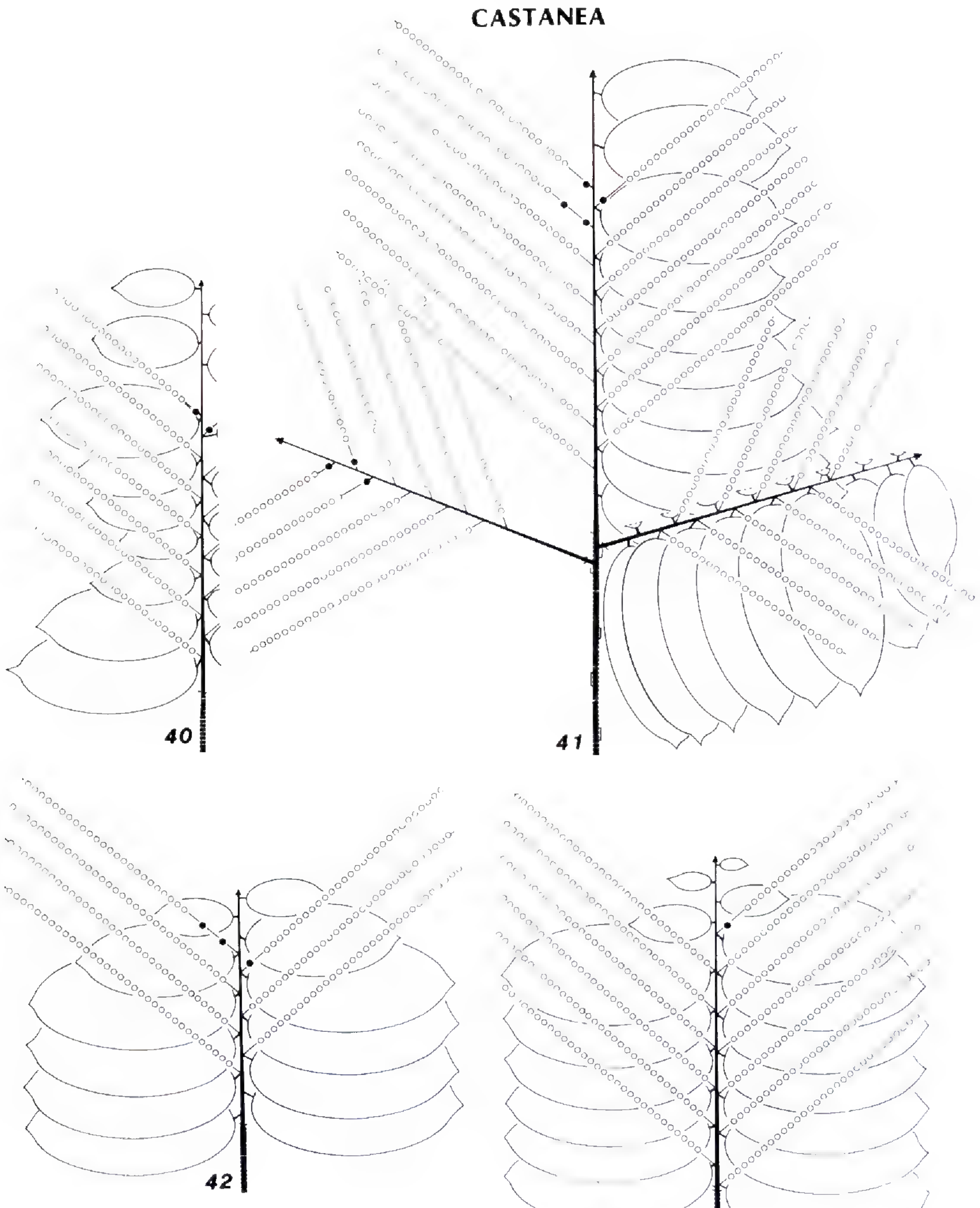
Sometimes sylleptic spikes and reproductive branches are accompanied by similar proleptic spikes and branches in a shoot system (e.g., FIGURES 16–19,



FIGURES 33–39. *Castanopsis* and *Quercus:* 33, *C. brevispina*; 34, *C. subacuminata*; 35, *C. stipitata*; 36, *C. stellatospina*; 37, 38, *C. chrysophylla*; 39, *Q. uraiana.*

30–32, 56). These proleptic structures are often strictly staminate, but the distal ones sometimes have a few pistillate flowers (e.g., FIGURES 6, 16–19, 31, 41, 46).

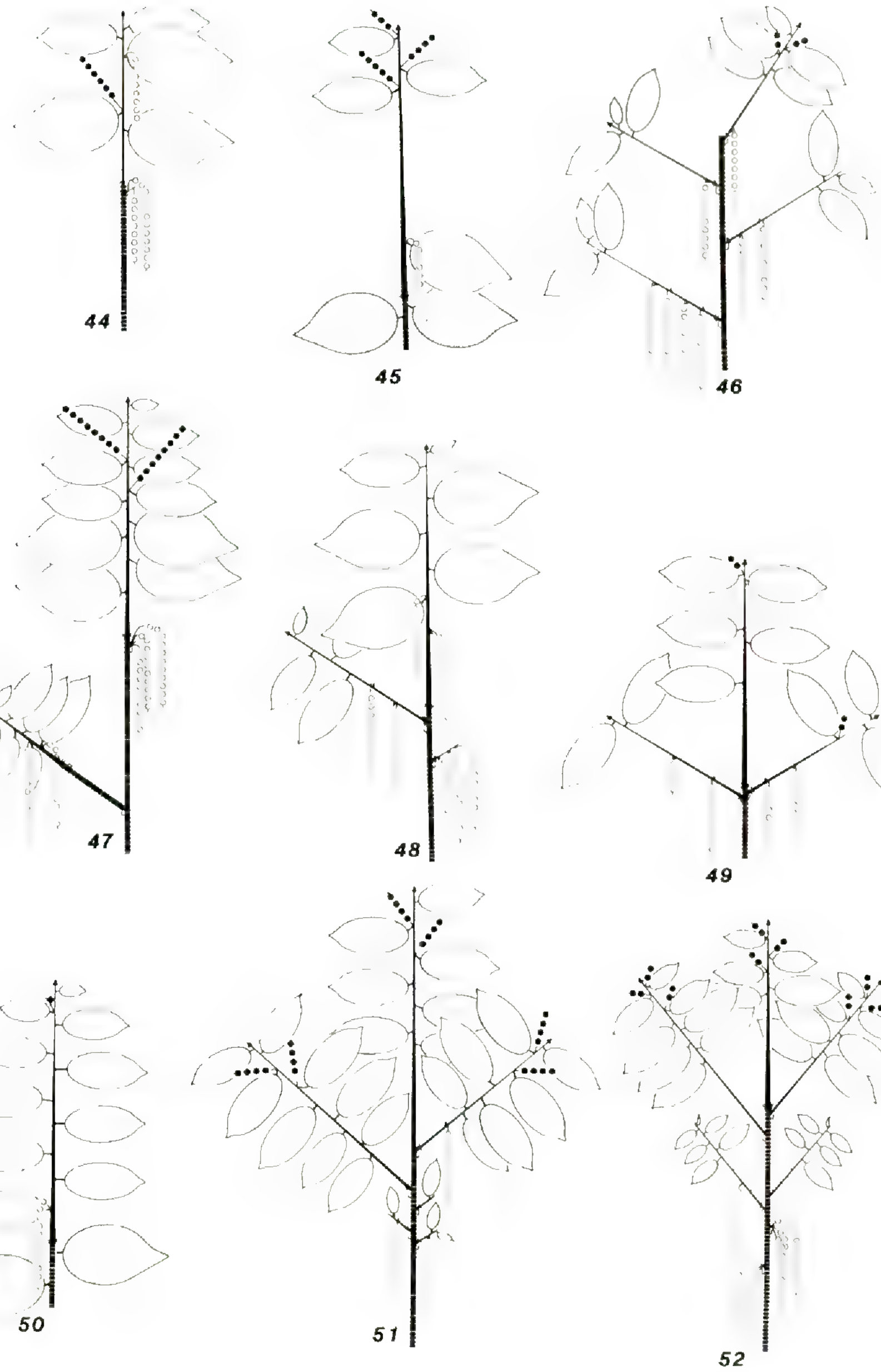
In some Fagaceae full repetition of the leader's growth pattern, floral display, and sex distribution is obvious in the branches, whether they are sylleptic or proleptic (FIGURES 10, 28, 31, 32, 41, 70A). In others the lateral branches are repetitive but determinate (FIGURE 26). More often, there is a basipetal gradient of decreasing similarity between the leader and its branches, both sylleptic and proleptic (FIGURES 25, 27–31, 33–35, 70C, D). The most extreme manifestation of this gradient has small, determinate, bracteose branches bearing only staminate spikes or catkins (e.g., FIGURES 25, 33–35, 44, 60, 70E–G). The middle branches, between the leader and the proximal branches, are frequently inter-



FIGURES 40–43. *Castanea:* 40, 41, *C. mollissima*; 42, *C. crenata*; 43, *C. dentata.*

mediate in structure as well; they are often folio-bracteose, bear a few pistillate flowers, and may be determinate or indeterminate.

The greatest differentiation between the leader and its branches occurs in *Quercus,* where in the most extreme cases some reproductive branches are distinctly short-shoots, are always proleptic and bracteose, bear only staminate catkins, and are entirely deciduous. The leader is foliose and bears pistillate spikes and sometimes also staminate catkins (FIGURES 44, 47, 52, 66, 70F, G). Less extreme differentiation is shown by branches that have catkins axillary to the proximal leaves or bracts while the distal part of the axis is foliose,

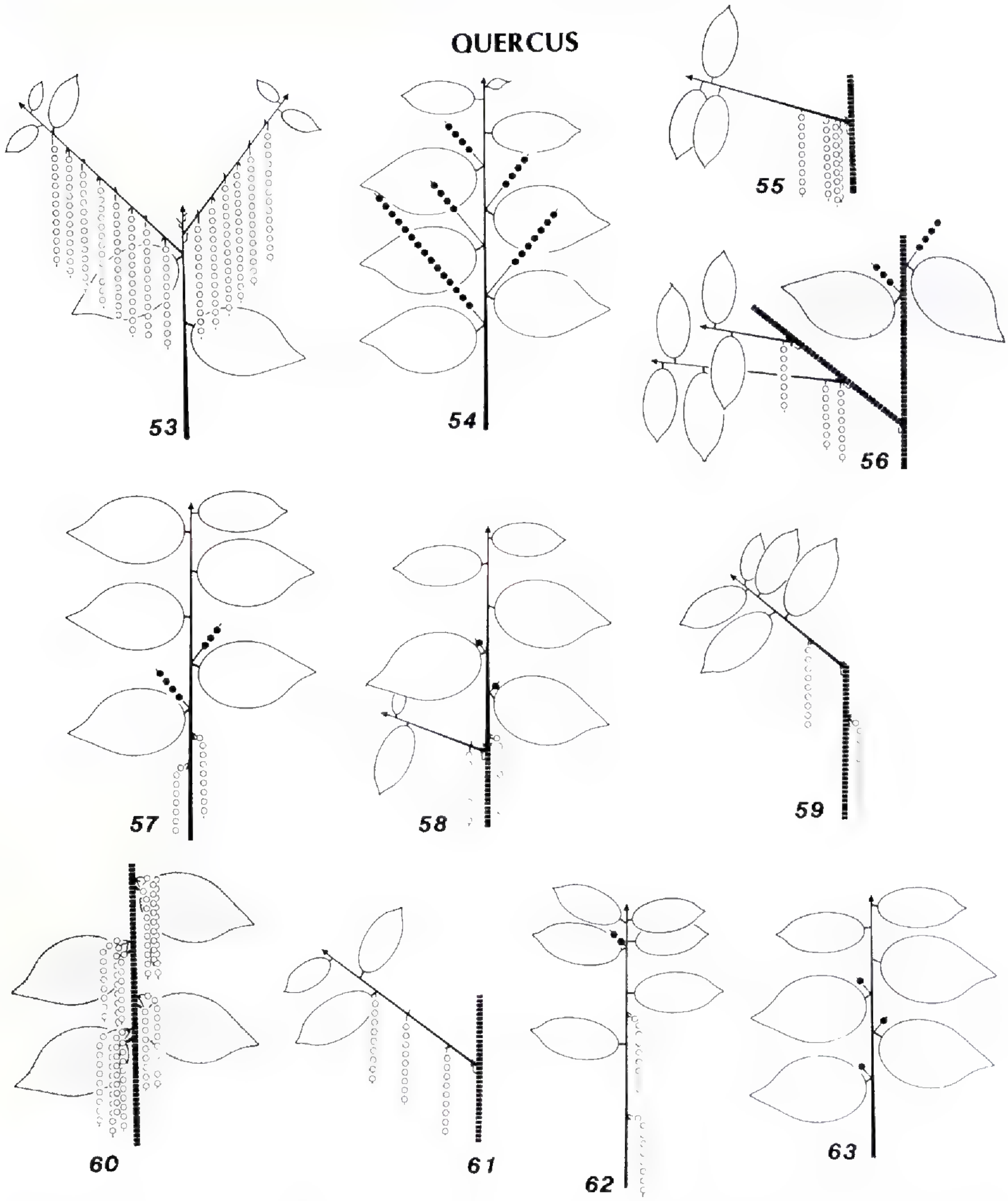


FIGURES 44–52. *Quercus:* 44, 47, *Q. glauca*; 45, *Q. championii*; 46, *Q. stenophylloides*; 48, *Q. morii*; 49, *Q. phillyraeoides*; 50, *Q. acuta*; 51, *Q. myrsinaefolia*; 52, *Q. gilva.*

sterile, and determinate or indeterminate (FIGURES 46–49, 55, 56, 64, 65). Sometimes several degrees of differentiation between leader and branches exist on the same tree.

DISTRIBUTION OF THE SEXES IN THE SHOOT SYSTEM

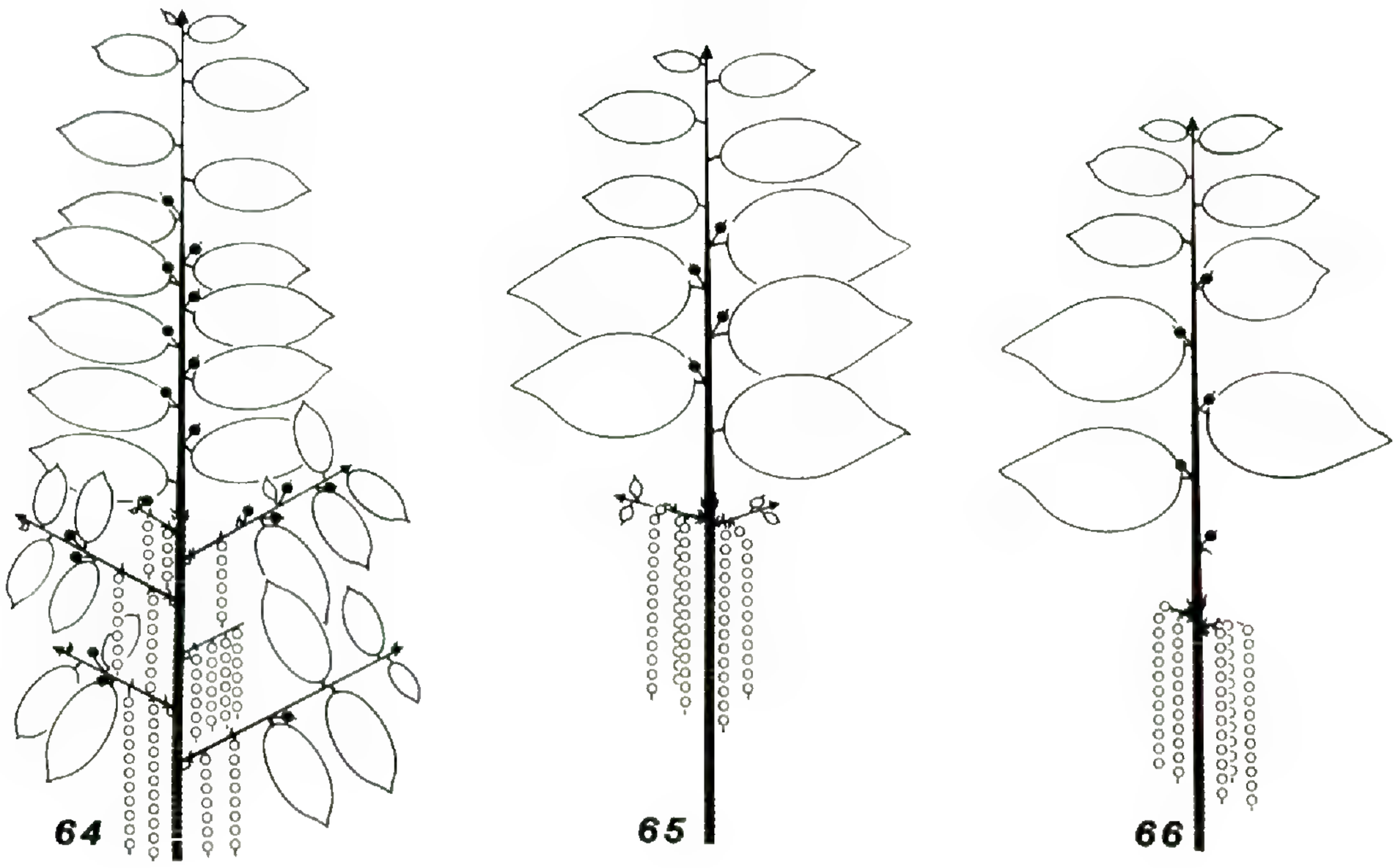
Pistillate flowers, if present at all in a shoot system, are borne on distal spikes; the proximal spikes are staminate (FIGURES 6–13, 16–23, 25–52, 54, 56–58,



FIGURES 53–63. *Quercus:* 53, *Q. kingiana*; 54, *Q. brandisiana*; 55, *Q.* cf. *chapensis*; 56, *Q. cambodiensis*; 57, *Q. mespilifolioides*; 58, *Q. griffithii*; 59, *Q. serrata*; 60, *Q. championii*; 61, *Q. kinabaluensis*; 62, *Q. valdinervosa*; 63, *Q. elmeri.*

62–66, 69, 70). Sometimes the leader has more pistillate flowers on more spikes than its branches (FIGURES 7, 10, 30, 70A–C), but in other cases the distribution of pistillate flowers is about equal on leader and branches (e.g., FIGURES 18, 26, 28, 31, 32). In any case, a clear acropetal gradient of increasing "femaleness" is evident in almost every species examined. This gradient is variously expressed in the leader, in the branches, and/or in the total inflorescence, and it complements the basipetal gradients of reduction of leaves to bracts and loss of indeterminacy in branches.

In *Quercus* and *Trigonobalanus daichangensis* the sexes are almost always borne on separate axes (FIGURES 44–66, 69). Pistillate spikes (which sometimes



FIGURES 64–69. *Quercus* and *Trigonobalanus:* 64, *Q. imbricaria*; 65, 66, *Q. borealis*; 67, 68, *T. verticillata*; 69, *T. daichangensis* (after Forman, 1964).

exist as a single cymule or flower) are invariably distal and are nearly always subtended by a leaf. Staminate catkins occur singly in the axil of a leaf or bract, mostly in the proximal part of the shoot system (FIGURES 44–53, 55–59, 61, 64–66, 69). They are shed soon after anthesis. Catkin-bearing short-shoots are proleptic (e.g., FIGURES 44, 47, 48, 52) and are also shed soon after anthesis.

In *Trigonobalanus verticillata* some shoots bear only staminate spikes, while others have androgynous ones (FIGURES 67, 68); our specimens and observations are inconclusive as to the existence of a sex gradient in the total inflo-

rescence. Likewise, information about sex distribution in *T. excelsa* is ambiguous. According to Lozano and colleagues (1979), staminate and pistillate inflorescences are borne separately on the tree.

In the northern genus *Castanea* (FIGURES 40–43) the ratio of staminate to pistillate cymules is higher than in *Castanopsis* or *Lithocarpus*. However, the only two American species of the latter two genera, *Castanopsis chrysophylla* (FIGURES 37, 38) and *Lithocarpus densiflora* (FIGURE 15) also have such a higher ratio, and they too are northern. This ratio apparently also exists in *Quercus*, where the northern species bear fewer pistillate cymules on a branch than do many tropical species.

SYLLEPSIS OF THE SPIKES

The spikes contain two kinds of axes: 1) an elongate primary axis or long-shoot to which the 2) cymose short-shoots are racemosely attached. Second-order sylleptic long-shoots are rather common in the staminate spikes of *Lithocarpus* and *Castanopsis chrysophylla* (FIGURES 7, 21–24, 37, 38, 67) and are occasional in *Castanea*. An occasional bisexual spike also has sylleptic branches (FIGURE 23). Such sylleptic branching produces ramified spikes with branches at what would otherwise be sites of cymules and each second-order long-shoot is subtended by a primary bract in the proper phyllotactic position (FIGURE 2). The truly sylleptic nature of this branching is evidenced in FIGURE 2, where second-order branches are appearing on an immature primary axis.

Sylleptically branched spikes differ from bracteose reproductive branches (as defined above) in that they bear dichasia on the primary axis and terminate in a floriferous axis. There is no functional or abortive bract-clad apex of the kind found on typical vegetative branches.

In some instances, typical bracteose reproductive branches bear a distal spike that overtops the primary axis (see FIGURE 26), and the abortive apex is then apparently lateral. Although such a branch appears to be a sylleptically branched spike, it is readily distinguished from a truly sylleptic spike by the large, lateral, bract-clad abortive apex.

DISCUSSION

Studies of floral development and morphology have produced a large body of literature on evolutionary pathways and adaptations in flowers. Although literature concerning inflorescences is less definitive, many of the same forces behind floral evolution are clearly also involved in inflorescence evolution, with analogous morphological results. Flowers and inflorescences share such major functions as effecting pollination and nurturing and disseminating seeds and fruits.

Such well-known floral evolutionary phenomena as pleiomery, oligomery, heterochrony, changes in size and symmetry, protogyny and protandry, and transfer of function are also found in inflorescences. We can therefore apply some of the principles of floral evolution to inflorescences.

In the history of plants, vegetative and reproductive functions became sep-

arated and strobili, flowers, and inflorescences were produced. Further phylogenetic differentiation in flowers was by continued separation of functions, producing such advanced features as imperfect flowers, dioecy, anemophily, or elaborate forms of entomophily, and a host of attendant morphological features. These have appeared repeatedly and independently in diverse angiosperms responding to similar evolutionary pressures. Apparent reversal of these trends, such as anemophily reverting to entomophily, involves further modifications of existing structures and behaviors in response to new evolutionary pressures similar to ancestral ones.

There is genetic and ecological evidence that the outcrossing produced by many of these structures and pollination systems is advantageous to the species. Temporal and/or spatial separation of the sexes is most evident in highly evolved plants such as the Fagaceae.

In the Fagaceae some evolutionary patterns have recurred at successively higher levels of morphological organization. The separation of sexes into different flowers, which is almost total in extant Fagaceae, preceded separation of imperfect flowers on the spike, of staminate from pistillate spikes on the same shoot, and of shoots bearing only staminate or pistillate spikes. Many stages of these events occur in various combinations in living Fagaceae, but of the genera studied, only *Quercus* and a few species in other genera show them in their fullest expression.

Paralleling these events are the beginnings of protandry at the inflorescence level. This is a natural consequence of the acropetal ontogeny of shoots and spikes, the acropetal anthesis of flowers, and the restriction of female flowers to distal regions of the shoots. None of the genera studied, however, is morphologically dioecious, although some may approach functional dioecism. The frequent lack of synchrony among adjacent conspecific individuals (which we often saw in the field) contributes another dimension to incipient functional dioecism.

The Fagaceae also show stages of separation of reproductive from vegetative functions. Foliose reproductive branches are usually indeterminate and perform all functions, including extension growth. Merely bracteose reproductive branches are mostly determinate and abscise quickly if they bear only staminate spikes, but they are determinate to indeterminate if they have pistillate flowers.

Compared with tropical species of Fagaceae, more northerly members show reduced or, most often, no syllepsis in their shoots or spikes. (The cymulose short-shoots are, of course, sylleptic on their long-shoots, as are spikes on the shoots that bear them.) The spikes of *Castanopsis chrysophylla* and *Lithocarpus densiflora* (and occasionally *Castanea*) show it only weakly. Even within *Castanopsis* and *Lithocarpus*, there is probably a general loss of syllepsis as one moves from the tropics into the Northern Hemisphere, while the strictly extratropical *Castanea* has nearly lost it altogether. In *Quercus* there is none in the catkins of any species we studied, and only one of our species, *Q. kingiana* from Burma (FIGURE 53), showed vegetative syllepsis.

These observations are consistent with the well-known decline of syllepsis in trees and shrubs in general as one moves northward from the tropics. It is thus possible that syllepsis is an ancestral condition in the Fagaceae and other

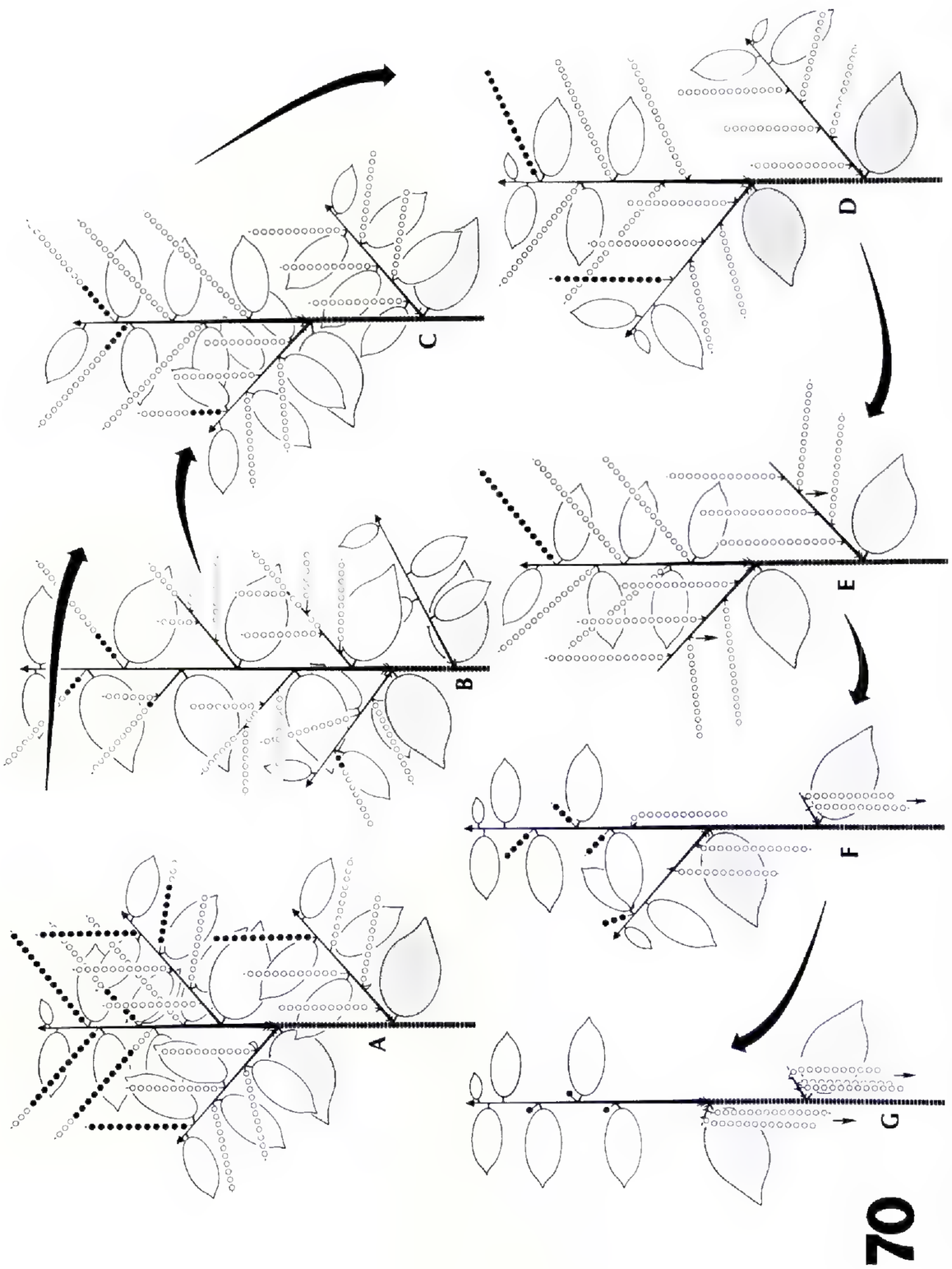


FIGURE 70. Possible derivations of inflorescence patterns in *Lithocarpus, Castanopsis, Castanea,* and *Quercus* (downward-pointing arrows indicate deciduous branches).

angiosperms, and that it was often reduced or lost in woody plants as they colonized cooler climates.

FIGURE 70 summarizes logical levels of specialization, based upon the concepts advanced above, in modern species of *Castanea, Castanopsis, Lithocarpus,* and *Quercus.* No hypothetical or extrafamilial patterns are shown. The coexistence of ancestral and derived characters among living members of such a large family is to be expected, although even the least derived stages (FIGURE 70A, B) are quite specialized for angiosperms. All the stages shown, as well as numerous intermediates and variants, are common in living Fagaceae and must be considered evolutionarily successful.

FIGURE 70A, B shows flowers of both sexes on some or all branches as well as on the leader—distributions common in *Lithocarpus* and *Castanopsis.* Some perfect flowers occur but are not indicated. Both illustrations also show proleptic and sylleptic indeterminate branches. The sylleptically branched staminate spikes of FIGURE 70B have perhaps preceded the condition in FIGURE 70C, where sylleptic branching is lost in both the leader and the spikes, and fertile branches are indeterminate with at least some exclusively staminate. Spikes are seldom ramified, and pistillate flowers are distal on the shoots but proximal on the spikes. This pattern occurs in *Castanea* (FIGURES 40–43) and some species of *Castanopsis.*

FIGURE 70D is similar to 70C, but the fertile portions of the branches are bracteose rather than foliose. Extension growth produces normal foliage leaves. The spikes are all unisexual. This pattern occurs in *Lithocarpus* (FIGURE 28) and *Castanopsis* (FIGURE 35).

In FIGURE 70E the branches are all proleptic and staminate. The upper branches are indeterminate, and the fertile region is bracteose. Lower branches are determinate and usually caducous. This combination of fertile determinate and indeterminate branches occurs in *Castanopsis* and *Lithocarpus.*

A common condition in Paleotropical *Quercus* is shown in FIGURE 70F. The leader has mostly pistillate spikes, and it sometimes has a few staminate catkins as well. Indeterminate branches can bear pistillate spikes and often have staminate catkins toward the base. Short-shoots bearing catkins are borne in leaf axils and are soon abscised.

The most extreme condition in extant Fagaceae is shown in FIGURE 70G and is commonest in northern *Quercus.* The pistillate spikes have one or few flowers. The leader lacks staminate catkins or has only a very few. The proximal branches are determinate, caducous short-shoots, and the distal branches are indeterminate. There are many variants of this and the preceding pattern.

The verticillate phyllotaxy and resultant verticillate display of inflorescences in *Trigonobalanus verticillata* is unique in the family, although some *Quercus* species produce crowded and essentially verticillate leaves near the end of a flush. Furthermore, *T. verticillata* produces alternate and then opposite leaves on many branches before forming whorled leaves with axillary inflorescences.

Forman (1964) believed the pendent catkins of *Quercus* and *Trigonobalanus daichangensis* to be derived from erect spikes of entomophilous Fagaceae, an opinion shared here and consistent with that of Schottky (1912). Forman (1964) also interpreted the single flowers on spikes and catkins of some *Quercus* and

TABLE 1. **Probable evolutionary trends in fagaceous inflorescences.**

CHARACTER	ANCESTRAL CONDITION	DERIVED CONDITION
1. Vegetative branching	sylleptic and proleptic	proleptic only
2. Branches	indeterminate, foliose	determinate, bracteose
3. Spike- and catkin-bearing branches	persistent	caducous
4. Flowers of spike-bearing branches	staminate and pistillate	staminate or pistillate
5. Flowers of leader	staminate and pistillate	pistillate only
6. Spikes	sylleptically branched	unbranched
7. Flowers of spikes	staminate and pistillate or perfect	staminate or pistillate
8. Staminate flowers borne in	spikes	catkins
9. Pistillate flowers on spikes	numerous	few or one
10. Pistillate flowers in total inflorescence	numerous	few to none

Trigonobalanus species as having been derived from dichasial clusters. *Trigonobalanus verticillata* and *T. excelsa* have dichasial flower clusters, while *T. daichangensis* has both clusters and single flowers. In addition, *T. daichangensis* has pendent catkins and is anemophilous, but the other two species have more or less erect male spikes and are probably entomophilous. Thus, *Trigonobalanus* is transitional between the entomophily of the Castaneoideae and the anemophily of *Quercus*.

Evolutionary increase in flower numbers is likely in some cases, especially in *Lithocarpus, Castanea,* and *Castanopsis*. On the other hand, there are fewer female flowers per spike and per total inflorescence in many northern Fagaceae. Catkins and spikes of *Quercus* generally bear fewer flowers than comparable axes of the other genera studied. Furthermore, there are reductions in floral and dichasial morphology in *Quercus*. The catkin can be interpreted as the least expensive structure, in terms of energy and materials, that can be produced quickly at the start of the relatively short temperate growing season. In addition, *Quercus* species in northern forests are conspecifically more gregarious and usually have fewer congeners than do species of *Lithocarpus, Castanopsis,* and *Quercus* in the tropics. In the north *Quercus* shows strong local conspecific pollination synchrony, while tropical *Lithocarpus* and *Castanopsis* (and perhaps *Quercus,* too) conspecifics frequently show marked reproductive asynchrony. The likelihood of successful pollination is thus perhaps as great in northern *Quercus* as in the other genera, which have more numerous flowers and are usually scattered in species-richer populations. The presence of relatively few species of *Quercus* in the lowland Paleotropics suggests that members of the genus have not been especially successful in migrating to warmer from cooler regions, where they probably originated. The converse is probably the case

with *Lithocarpus* and *Castanopsis,* both of which have fewer temperate than tropical species.

TABLE 1 summarizes likely evolutionary trends in fagaceous inflorescences, as portrayed in FIGURE 70. Intermediates and combinations of these characters can be found in many species and sometimes on a single individual. Within flower and fruit characters, ecology, and geography, there are correlates to these inflorescence characters but our data are as yet inconclusive. We suspect that inflorescence characters and fruit size are related. The range in dry-fruit weight in our Paleotropical specimens is from less than 0.5 to more than 60 g.

A few extant Fagaceae bear pedunculate pistillate cymules (e.g., FIGURES 1, 6, 8) that are perhaps indicative of ancestral thyrselike conditions. Soepadmo (1972) considered *Lithocarpus elegans* (Blume) Hatus. ex Soep. to be probably the most primitive in its genus. It has staminate cymules with up to 24 flowers, and pistillate ones with up to 10; the staminate spikes are frequently much branched. Hjelmqvist (1948) regarded *Lithocarpus* as the primitive genus in the family based on characters of the flowers and cymules. Our observations of inflorescences support that conclusion.

The Betulaceae are sometimes cited as the closest living relatives of the Fagaceae. Abbe (1935) showed the possible derivation of betulaceous inflorescences from thyrselike predecessors, a pattern perhaps similar to that of the Fagaceae. Jäger (1980) analyzed betulaceous inflorescences and postulated reduction in number and size of catkins, increase in winter protection of catkins, and reduction of leaf size, all associated with adaptation to colder climates with shorter growing seasons. The more primitive Betulaceae occur in warmer Sino-Himalayan areas. These attributes parallel those of the Fagaceae to some extent, but the Betulaceae are generally more northern and lack large numbers of tropical or subtropical species that might be of value for comparison. Further, there are no entomophilous Betulaceae.

Many inflorescence characters of the Fagaceae parallel those found by Manning (1938) in the Juglandaceae. That family exhibits trends 4–10 shown in TABLE 1. There are also geographic correlations of structure that point strongly to congruent biogeographic histories of the two families.

Čelakovský (1889) analyzed inflorescence patterns in the Fagaceae, Betulaceae, and Juglandaceae and found strong tendencies for proleptic shoots to be reproductive and bear reduced leaves. He interpreted single perfect flowers in leaf axils as primitive in these families' ancestors. In our study we have applied the principles of differentiation used by Čelakovský, with some modifications. We believe that he was correct in his assessment of fagaceous inflorescences, although his conclusions were based on only a few species. Further, we agree that the single perfect axillary flower is the primitive condition for angiosperms. The flower as a reproductive short-shoot is but one of a series of evolutionary repetitions of the tendencies to concentrate and elaborate reproductive structures.

ACKNOWLEDGMENTS

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APPENDIX. **Species studied and provenance of specimens.**

CASTANEA	
C. crenata Sieb. & Zucc.	Taiwan (cultivated)
C. dentata Borkh.	Nebraska (cultivated)
C. mollissima Blume	Nebraska (cultivated)
CASTANOPSIS	
C. acuminatissima (Blume) A. DC.	Vietnam
C. argyrophylla King	Thailand
C. armata Spach	Thailand
C. brevispina Hayata	Taiwan
C. chevalieri Hickel & A. Camus	Vietnam
C. chrysophylla (Douglas) A. DC.	California, Oregon
C. costata (Blume) A. DC.	Borneo (Sabah)
C. cuspidata Schottky	Japan
C. echinocarpa A. DC.	Thailand
C. ferox Spach	Thailand
C. fissa (Champ.) Rehder & Wilson	Hong Kong
C. formosana (Skan) Hayata	Taiwan
C. foxworthyi Schottky	Borneo (Sabah)
C. inermis (Lindley) Bentham & Hooker f.	Malaya
C. javanica (Blume) A. DC.	Indonesia (Java)
C. lanciifolia (Roxb.) Hickel & A. Camus	Thailand

C. longipetiolata Hickel & A. Camus	Cambodia
C. megacarpa Gamble	Malaya
C. motleyana King	Borneo (Sarawak)
C. nephelioides King ex Hooker f.	Malaya
C. philippinensis (Blanco) Vidal	Philippines
C. cf. *pierrei* Hance	Thailand
C. pyriformis Hickel & A. Camus	Vietnam
C. purpurea Barnett	Thailand
C. rhamnifolia (Miq.) A. DC.	Thailand
C. schefferiana Hance	Malaya
C. stellatospina Hayata	Taiwan
C. stipitata Hayata	Taiwan
C. subacuminata Hayata	Taiwan
C. tribuloides (Smith) A. DC.	Burma
C. tungurrut (Blume) A. DC.	Indonesia (Java)
LITHOCARPUS	
L. aggregata Barnett	Thailand
L. amygdalifolia (Skan) Hayata	Taiwan
L. bennettii (Miq.) Rehder	Borneo (Sabah)
L. bolovensis A. Camus	Cambodia
L. brevicaudata Hayata	Taiwan
L. buddii (Merr.) A. Camus	Philippines
L. cantleyana (King) Rehder	Singapore
L. caudatifolia (Merr.) Rehder	Borneo (Sabah), Philippines
L. celebica (Miq.) Rehder	Philippines
L. clementiana (King ex Hooker f.) A. Camus	Borneo (Sarawak)
L. conocarpa (Oudem.) Rehder	Singapore
L. cooperta (Blanco) Rehder	Philippines
L. cornea (Lour.) Rehder	Hong Kong
L. curtisii (King ex Hooker f.) A. Camus	Malaya
L. dasystachya (Miq.) Rehder	Borneo (Sabah, Sarawak)
L. dealbata (Hooker f. & Thomson) Rehder	Burma, Thailand
L. densiflora (Hooker & Arn.) Rehder	California, Oregon
L. echinocarpa A. Camus	Vietnam
L. edulis Nakai	Japan
L. elegans (Blume) Hatus. ex Soep.	Thailand
L. ewyckii (Korth.) Rehder	Borneo (Sabah)
L. fenestrata (Roxb.) Rehder	Burma
L. formosana Hayata	Taiwan
L. garrettiana (Craib) A. Camus	Thailand
L. gracilis (Korth.) Soep.	Borneo (Sabah)
L. hancei (Bentham) Rehder	Hong Kong
L. harmandii (Hickel & A. Camus) A. Camus	Cambodia
L. havilandii (Stapf) Barnett	Borneo (Sabah)
L. hendersoniana A. Camus	Malaya
L. hystrix (Korth.) Rehder	Malaya
L. kawakamii Hayata	Taiwan
L. kodaihoensis Hayata	Taiwan
L. konishii (Hayata) Hayata	Taiwan
L. lampadaria (Gamble) A. Camus	Malaya
L. leptogyne (Korth.) Soep.	Borneo (Sarawak)
L. lucida (Roxb.) Rehder	Malaya
L. macphailii (M. R. Henderson) Barnett	Malaya
L. maingayi (Bentham) Rehder	Malaya

L. meijeri Soep.	Borneo (Sabah)
L. mindanaënsis (Elmer) Rehder	Philippines
L. nantoensis Koidz.	Taiwan
L. neorobinsonii A. Camus	Malaya
L. nieuwenhuisii (Seemen) A. Camus	Borneo (Sabah)
L. nodosa Soep.	Borneo (Sabah)
L. papillifer Hatus. ex Soep.	Borneo (Sabah)
L. pattaniensis Barnett	Malaya
L. polystachya (Wallich) Rehder	Thailand
L. rassa (Miq.) Rehder	Malaya
L. reinwardtii A. Camus	Cambodia
L. rhombocarpa Hayata	Taiwan
L. rufovillosa Soep.	New Guinea
L. soleriana (Vidal) Rehder	Philippines
L. sootepensis (Craib) A. Camus	Thailand
L. sundaica (Blume) Rehder	Borneo (Sarawak)
L. ternaticupula Hayata	Taiwan
L. thomsonii (Miq.) Rehder	Thailand
L. truncata (King ex Hooker f.) Rehder & Wilson	Burma
L. turbinata (Stapf) Forman	Borneo (Sabah)
L. urceolaris (Jack) Merr.	Borneo (Sabah)
L. wallichiana (Lindley ex Hance) Rehder	Malaya
L. woodii (Hance) A. Camus	Philippines
L. wrayi (King) A. Camus	Thailand
QUERCUS	
Q. acuta Thunb.	Japan
Q. borealis Michaux	Nebraska
Q. brandisiana Kurz	Burma, Thailand
Q. cambodiensis Hickel & A. Camus	Cambodia
Q. championii Bentham	Hong Kong
Q. chrysolepis Liebm.	Oregon
Q. elmeri Merr.	Borneo (Sabah)
Q. gilva Blume	Japan, Taiwan
Q. glauca Thunb.	Taiwan
Q. griffithii Hooker f. & Thomson	Thailand
Q. imbricaria Michaux	Iowa
Q. kinabaluensis Soep.	Borneo (Sabah)
Q. kingiana Craib	Burma
Q. lanata Smith	Vietnam
Q. lowii King	Borneo (Sabah)
Q. merrillii Seemen	Borneo (Sarawak)
Q. mespilifolioides A. Camus	Thailand
Q. morii Hayata	Taiwan
Q. myrsinaefolia Blume	Japan
Q. pachyloma Seemen	Taiwan
Q. paucidentata Franchet	Japan
Q. phillyraeoides A. Gray	Taiwan
Q. salicina Blume	Japan
Q. serrata Thunb.	Japan, Thailand
Q. stenophylloides Hayata	Taiwan
Q. subsericea A. Camus	Borneo (Sabah)
Q. uraiana Hayata	Taiwan
Q. valdinervosa Soep.	Borneo (Sabah)
Q. virginiana Miller	Florida

TRIGONOBALANUS *T. verticillata* Forman	Borneo (Sabah)

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THE ARCHITECTURE OF DEVIL'S WALKING STICK, ARALIA SPINOSA (ARALIACEAE)

PETER S. WHITE

ARALIA SPINOSA L., a small tree of moist sites in eastern deciduous forests, is striking in appearance. Among its distinctive traits are large, two- or three-times compound leaves (often over 1 m long and with more than 100 leaflets), abundant prickles, large terminal inflorescences (over 6000 flowers), and a relatively unbranched pachycaulous habit. Several of these characteristics are treated in the empirical observations known as Corner's rules (Hallé *et al.*, 1978), which state that the thicker the annual increment, the larger the leaf borne on the increment and the fewer the ultimate number of branches. A test of Corner's rules in eastern deciduous trees (P. S. White, 1983) confirmed that *Aralia* is extreme in form: it had larger leaves, thicker annual increments, and fewer branches per unit leaf area than any of the other 47 species considered. The ecological role of *Aralia* is also of interest. Although trees of this species sometimes persist in shade, they occur primarily in disturbed areas (where they appear after fire, windstorm, or gap creation) and in old fields.

The relationship between the architecture and the ecological role of a tree has been the subject of a growing literature (e.g., Horn, 1971; Whitney, 1976; Givnish, 1978a; Hallé *et al.*, 1978). *Aralia* was selected for study because several of its morphological traits (large annual increment (Marks, 1975), high numbers of leaves and extensive total leaf area per annual increment (P. S. White, 1983), and larger leaf size with compound organization (Givnish, 1978a, 1978b)) have been hypothesized to be correlates of shade intolerance.

In this study I investigated the gross morphology and life history of *Aralia* ramets. Of primary interest were the growth in height and in diameter of individual ramets, the accumulation of branches in *Aralia* crowns over time, and the leaf area carried by these branches.

METHODS

Three populations of *Aralia spinosa* occupying moist, low-elevation (500–600 m) sites in the Great Smoky Mountains, Sevier County, Tennessee, were sampled. These populations were irregular in extent due to past agricultural disturbances. Since *Aralia spinosa* is clonal, individual stems are ramets; genets were not distinguished here because this would have greatly disturbed the populations. A random-numbers table was used to sample 114 ramets—one-fourth of all stems encountered.

Because leaf scars, terminal bud-scale scars, and inflorescence axes all persist

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for ten to fifteen years, the developmental history of each ramet could be reconstructed. For each year of growth, the amount of extension growth (the annual increment, or the length of axis produced per year), the number of leaves (on stems older than one year, the number of leaf scars), and the presence or absence of flowering (as shown by the position of old inflorescence axes) were recorded. Analysis of architectural development was facilitated because flowering and branching are intimately related: each flowering event terminates the growth of the axis, with branching occurring the following year from axillary buds that develop below the old inflorescence axis.

Each year's increment was numbered starting at the base of the ramet (annual increment no. 1) and working to the tips of the branches (the most recent year's growth) (see FIGURE 1). Yearly increments were also numbered from the base of each branch order. In this way, the increment formed each year could be analyzed as a function of age and crown position.

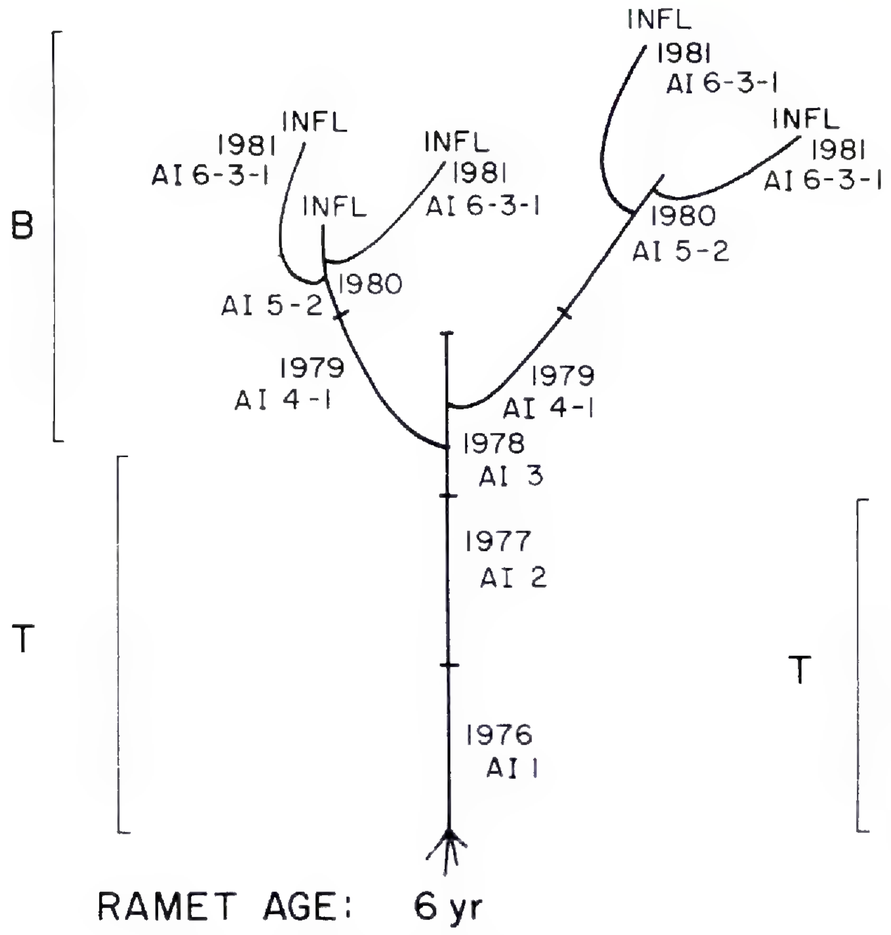
The numbering system was used to divide annual increments into trunk increments ("T" in the figures; the unbranched parts of the ramet) and first- and subsequent-order branch increments ("B" in the figures). Spur branches ("Sp"; short, slow-growing, suppressed branches) were so morphologically distinctive that they were segregated from other branches in the analysis, as were inflorescence axes ("F").

Part of one population had been cut during roadside mowing the previous season (1980). The trunks that sprouted after this grew more vigorously than did uninjured trunks. Shaded stems, on the other hand, grew less vigorously than did uninjured ones. Hence, for the trunk-building phase of growth, three states could be contrasted: injured, open-grown ("I" in the figures), uninjured, open-grown ("T"), and uninjured, shaded ("S"). For comparisons between trunks and branches, only open-grown, uninjured trunks ("T") were used. Note that the "T" (uninjured, unsuppressed trunks) in the figures was used twice: once in the "T" vs. "B" (branches), "F" (inflorescences), and "Sp" (spur branches) comparison, and again in the "T" vs. "I" (injury sprouts) and "S" (shaded plants) comparison. The data labeled "T" are identical in these separate comparisons.

Bifurcation ratios (Whitney, 1976) were computed for ramets. This is the average number of daughter branches per branch, using a branch-ordering scheme similar to that used in stream ordering (Whitney, 1976). Branch angles were measured at the base of each branch. Due to distal, adaxial bending of the branch, however, effective branch spread was less than that predicted from basal branch angles. Hence, effective branch angle (in degrees) was computed from branch length and the spread of the branch tip away from the axis of the next lower branch order.

Since *Aralia spinosa* is deciduous, leaves could only be measured on the most recent year's growth. A random-numbers table was used to select one leaf from each of the leafy shoots present. This leaf was characterized in terms of the annual-increment numbering system described above; leaf length and width (outer points of the outline of the compound leaf) and number of leaflets were recorded. Fifty trunk and fifty branch leaves were sampled. A subsample

ANNUAL INCREMENT NUMBERING SYSTEM



KEY TO ANNUAL INCREMENT NUMBERS (AI)

6	—	3	—	1
6th AI from base of plant		3rd AI from base of first order branch		1st AI of a second order branch

- AI - Annual Increment number
- 1976, etc. - Year of growth
- INFL - Position of inflorescence
- T - Trunk
- B - Branch
- ✗ - Terminal bud position or scars

FIGURE 1. Annual increment ("AI") numbering system used to model growth and branching of *Aralia spinosa*.

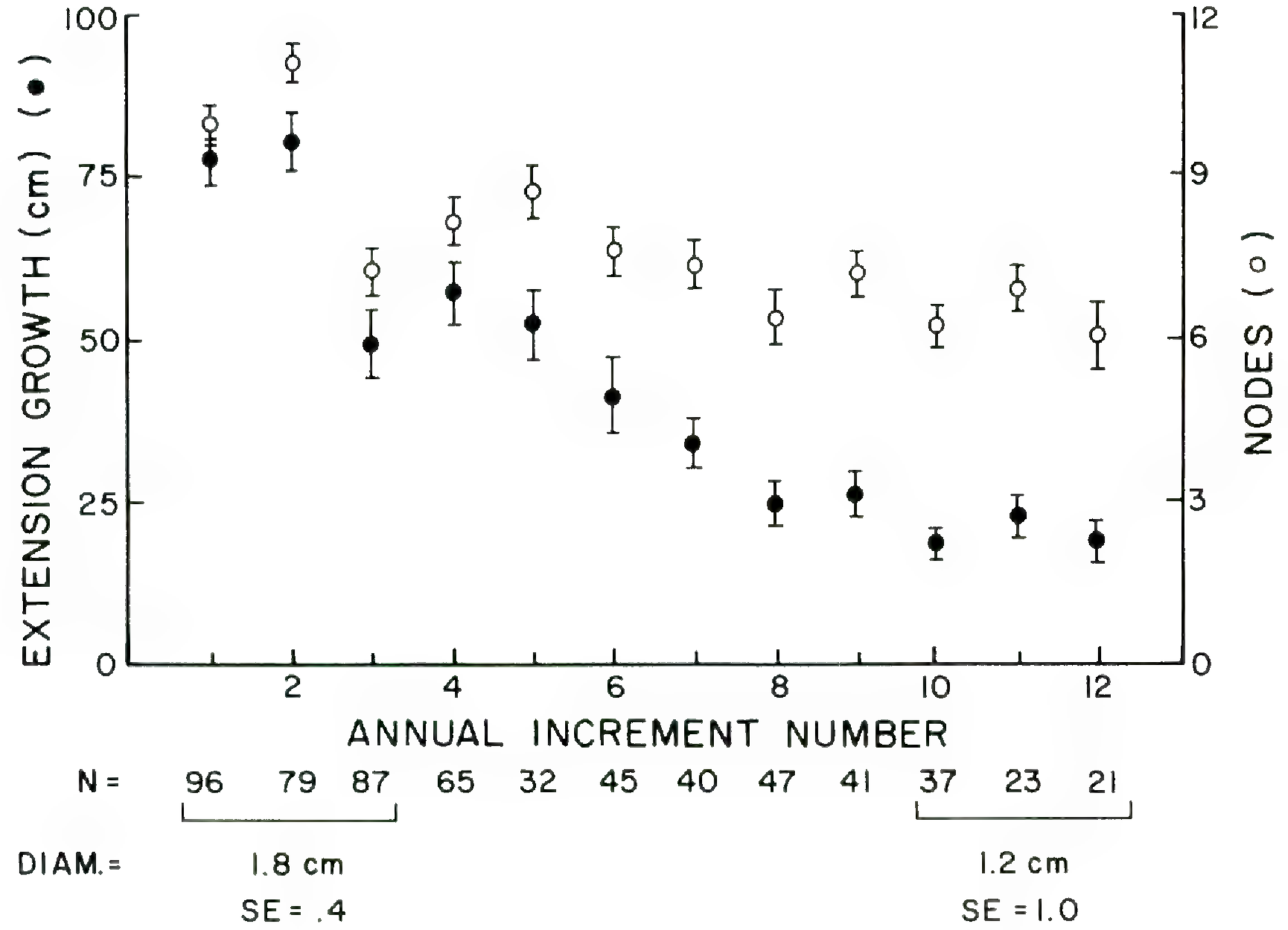


FIGURE 2. Mean length of increment (extension growth) and mean number of leaves (nodes) borne per year in *Aralia spinosa* as function of annual increment number. Mean diameters of 3 lowermost and 3 uppermost annual increments shown beneath figure; standard errors indicated above and below means.

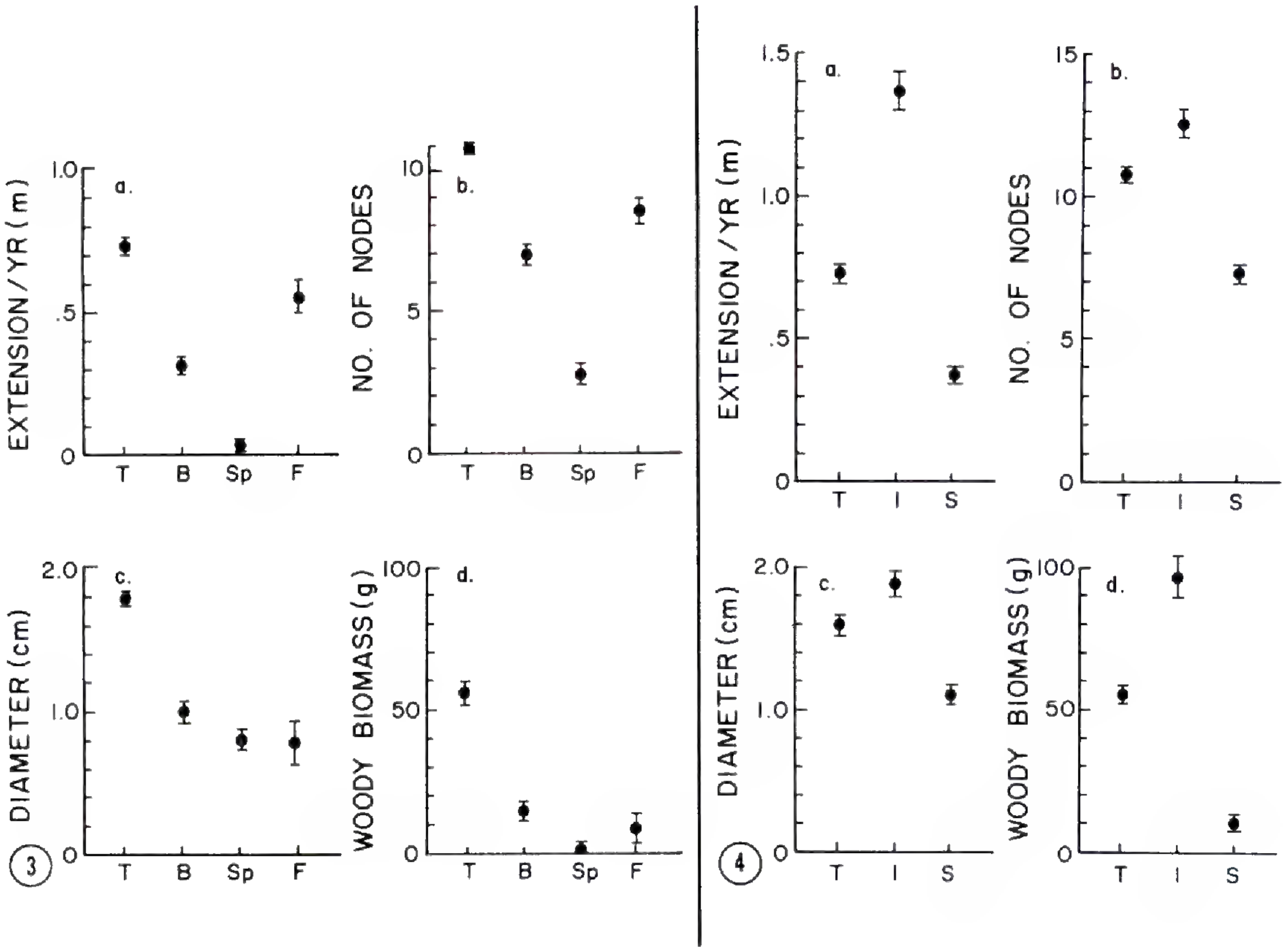
of leaflets was used to establish a regression between leaflet blade area and dry weight.

Diameters of the most recent year's growth (one-year-old shoots) and of the basal increment of the ramet (annual increment no. 1) were measured. A subsample of ramets was harvested for determination of biomass of wood, leaves (divided into leaflet blades and rachides), inflorescences, and infructescences. These biomass samples were randomly selected from within the different age classes of the ramets studied. They were oven dried at 105°C until their weight stabilized (usually after 48 hours) and then weighed.

RESULTS

EXTENSION GROWTH, DIAMETER, BIOMASS, AND NUMBER OF LEAVES PER SHOOT

For each of the first two years, extension growth in *Aralia* averaged more than 75 cm; this was followed by a decline, so that by the eighth to tenth years extension growth averaged less than 25 cm annually (a 67% decline; FIGURE 2). The average diameter of annual increments also decreased (FIGURE 2, below). Additionally, the number of leaves borne per year ("nodes" or leaf scars present; FIGURE 2) declined, but the decline—ca. 40 percent—was less steep



FIGURES 3, 4. 3, characteristics of annual increments as function of position on plant (T = trunk, B = branches, Sp = spurs, F = inflorescence axes): a, mean extension growth; b, mean number of nodes; c, mean diameter; d, mean woody biomass. 4, characteristics of trunk increments as function of shading and injury (T = open-grown, uninjured trunks, I = trunk segments sprouting after injury during previous season, S = shaded plants): a, mean length of increment; b, mean number of nodes; c, mean diameter; d, mean woody biomass. Standard errors indicated above and below means.

than that for extension growth (early growth averaged about 10 leaves per increment, while later increments had about 6). This decrease in extension growth and leaf number with age corresponded to the first flowering and branching of the stem. The stage of rapid height growth, high leaf numbers per annual increment, and sterility was termed the "trunk-building phase." Growth is strictly erect and unbranched during this phase.

Mean differences between trunks and branches for extension growth, and for number of leaves, diameter, and biomass per (new) annual increment, were all significant at the .001 level (FIGURE 3). Trunk annual increments averaged .7 m in extension growth, 10.7 leaves, 1.8 cm in diameter, and 56.2 g woody biomass; branch annual increments averaged .31 m in extension, 7.01 leaves, 1 cm in diameter, and 15.1 g. Spur branches showed the lowest extension growth (.02 m), the lowest number of leaves (2.9), and the lowest first-year woody biomass (.5 g). Diameters of branches, spurs, and inflorescence axes were not significantly different (FIGURE 3).

Trunks that resprouted after injury grew to larger dimensions than uninjured ones (FIGURE 4): they averaged almost twice the extension growth (1.4 m) in

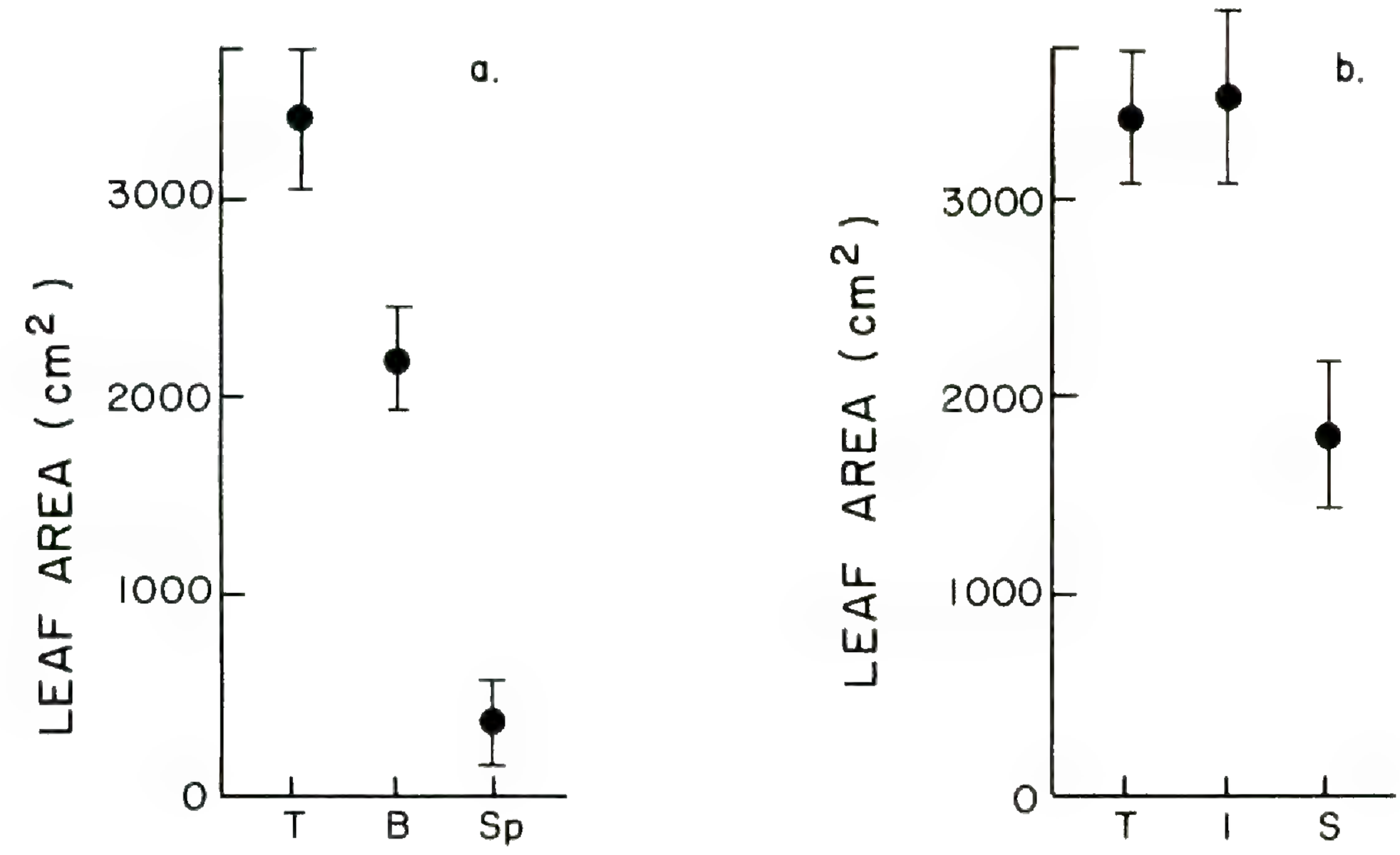


FIGURE 5. Mean surface area of individual leaf blades: a, open-grown individuals (T = trunks, B = branches, Sp = spurs); b, trunks (T = open-grown trunks, I = ramets sprouting after injury during previous season, S = shaded ramets). Standard errors shown above and below means.

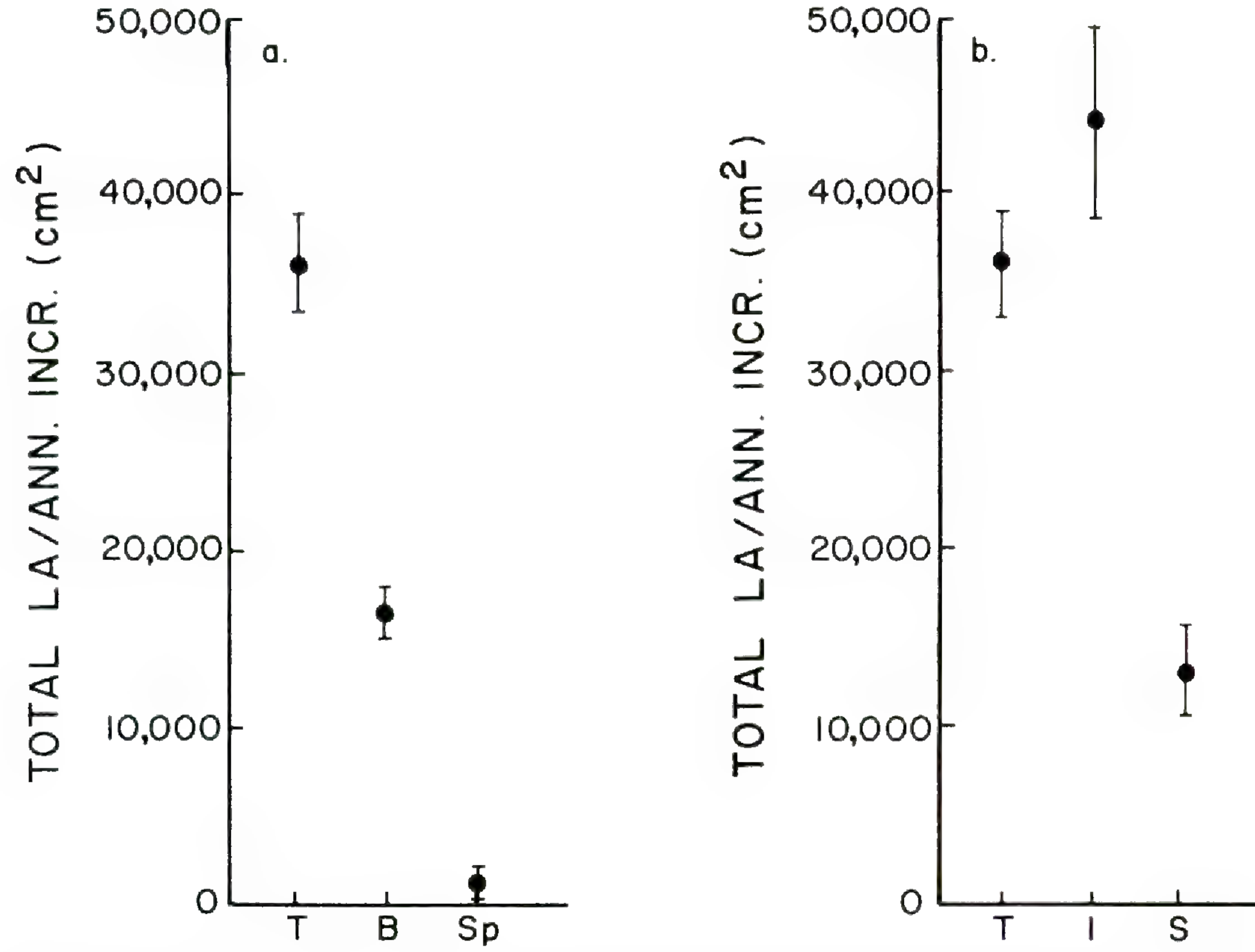


FIGURE 6. Mean total leaf area per annual increment: a, open-grown individuals (T = trunks, B = branches, Sp = spurs); b, trunks (T = open-grown, uninjured trunks, I = ramets sprouting after injury during previous season, S = shaded ramets). Standard errors shown above and below means.

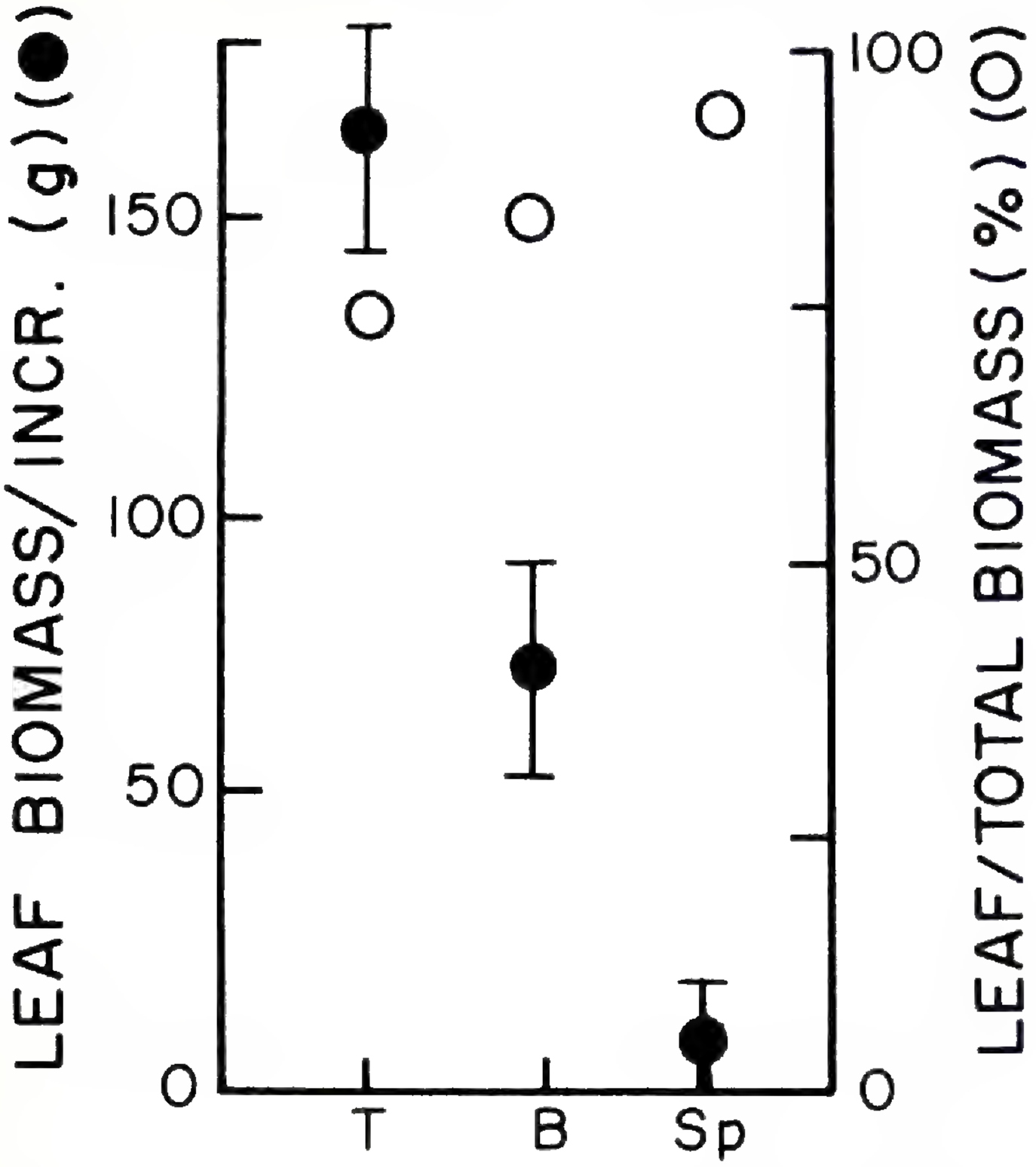


FIGURE 7. Mean leaf biomass per annual increment (left) and leaf biomass as percentage of total annual increment biomass (right). Data for open-grown, uninjured ramets (T = trunks, B = branches, Sp = spurs). Standard errors shown above and below means.

the first year after injury, and they had greater leaf numbers (12.6), diameters (1.9 cm), and woody biomass (97.9 g). Shaded ramets had the lowest values for these characteristics (.4 m extension, 7.2 leaves, 1.1 cm diameter, and 10 g woody biomass). These means were significantly different at the .01 level.

LEAF CHARACTERISTICS

Leaves borne on trunks averaged 3333 cm^2 in area—significantly larger ($P < .001$) than those borne on either branches (2295 cm^2; a 31% decline) or spurs (only 300 cm^2; FIGURE 5, a). For trunks, leaves were smaller on shaded individuals (1850 cm^2) than on open-grown ones, but trunks growing after injury were not significantly different than uninjured ramets (FIGURE 5, b). Trunk leaves (uninjured, open grown) averaged 1.02 m long (SD = .2) and 95.1 leaflets (SD = 27.8), while branch leaves averaged .86 m long (SD = .18) and 77.3 leaflets (SD = 27).

Total leaf area per annual increment (mean area per leaf times mean number of leaves per increment) showed the same trends: trunk increments bore over 35,000 cm^2 total leaf area, while branch increments bore ca. 17,000 cm^2, and spurs bore less than 1000 cm^2 (differences significant at the .001 level; FIGURE 6, a). Injured ramets had a greater total leaf area per increment than uninjured ones because of higher leaf numbers per increment (FIGURE 6, b).

TABLE 1. **Mean number of branches borne as a function of branch order.**

BRANCH ORDER*	MEAN NUMBER OF BRANCHES BORNE	SE
1 (N = 42)	2.7	.17
2 (N = 116)	1.6	.06
3 (N = 125)	1.4	.05
4 (N = 121)	1.5	.06
5 (N = 82)	1.3	.07
6 (N = 47)	1.4	.15
7 (N = 22)	1.2	.09
8 (N = 5)	1.4	.27

*Branch order 1 is the first branching event.

Total leaf biomass per annual increment, therefore, declined from trunks to branches (FIGURE 7). However, woody biomass per successive annual increment decreased more quickly than leaf weight; hence, if leaf biomass is expressed as a percentage of total biomass per annual increment (FIGURE 7, right), relative leaf biomass actually increased from trunks to branches and was highest in spur branches. It should also be borne in mind that branched plants had several to many new shoots; hence, total leaf biomass per ramet (as opposed to leaf biomass per annual increment as discussed above) increased through the life of the plant with the increase in the number of branches in the crown.

Three tissues were weighed separately in one-year-old annual increments: leaflet blades, rachides, and wood. There was an average of 2.5 g of leaflet-blade tissue and 1.3 g of rachides per g of woody tissue. Total leaf biomass was thus 3.8 g per g of woody tissue. Leaflet-blade biomass per g of supportive biomass (rachides plus wood) was 1.1 g.

FLOWERING AND BRANCHING

At first flowering, the mean age was 3.54 years and the mean height (to the base of the inflorescence) 2.6 m. This marked the end of the trunk-building

TABLE 2. **Frequency of flowering in branches as a function of age.***

	PERCENT FLOWERING		
Branch age at flowering† (years)	**All branches** (N = 686)	**First-order branches** (N = 127)	**All subsequent-order branches** (N = 559)
1	57.5	26.8	64.4
2	39.6	73.2	32.4
3	2.3	—	2.9
4	0.6	—	0.4

*No spurs were included in these data.

†Branch age was determined as follows: the first annual increment of a particular branch order was year 1 for that branch, the second annual increment was year 2, and so on, until flowering.

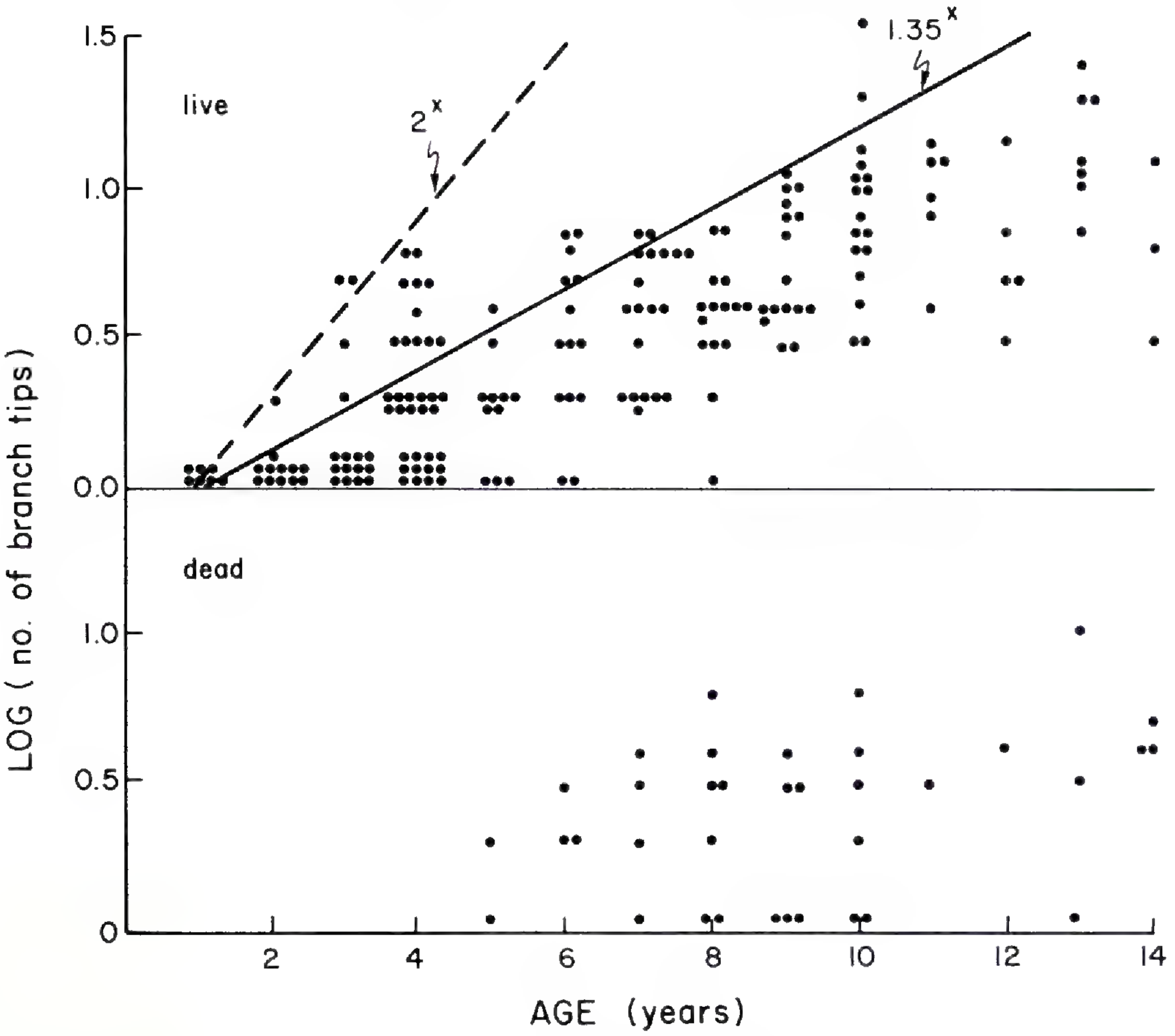


FIGURE 8. Accumulation of live (above) and dead (below) branches in *Aralia spinosa* as function of ramet age. Spurs not included. Straight line labeled 2^x corresponds to theoretical addition of 2 branches each year, characterizing early life history of *Rhus typhina*; that labeled 1.35^x corresponds to model for *Aralia spinosa*, $b = 1.35^x$ (b = number of branch tips, x = ramet age in years).

phase; the apex died and lateral buds below the inflorescence were the source of branches and hence of extension growth the following year. Two factors controlled the rate of branch increase as the ramets aged: the number of branches (axillary buds) that developed the year after flowering, and the number of years that these branches remained sterile before they flowered and produced higher-order branching. The first branching event was unlike the others in both of these characteristics (TABLES 1, 2). The year following the first time an individual ramet flowered, an average of 2.7 branches were produced. Subsequent flowering events produced only 1 or 2 branches (mean = 1.2–1.6—significantly different from means for primary branches at the .01 level; TABLE 1). First-order branches usually remained sterile for at least one year (26.8% flowered the first year), while later ones were more likely (64.4%) to flower their first year of development.

Branch longevity (before flowering) and branches per flowering event controlled accumulation of branches over time (FIGURE 8). Two reference lines are shown: *Rhus typhina* L., in its early life, accumulated branches at the rate

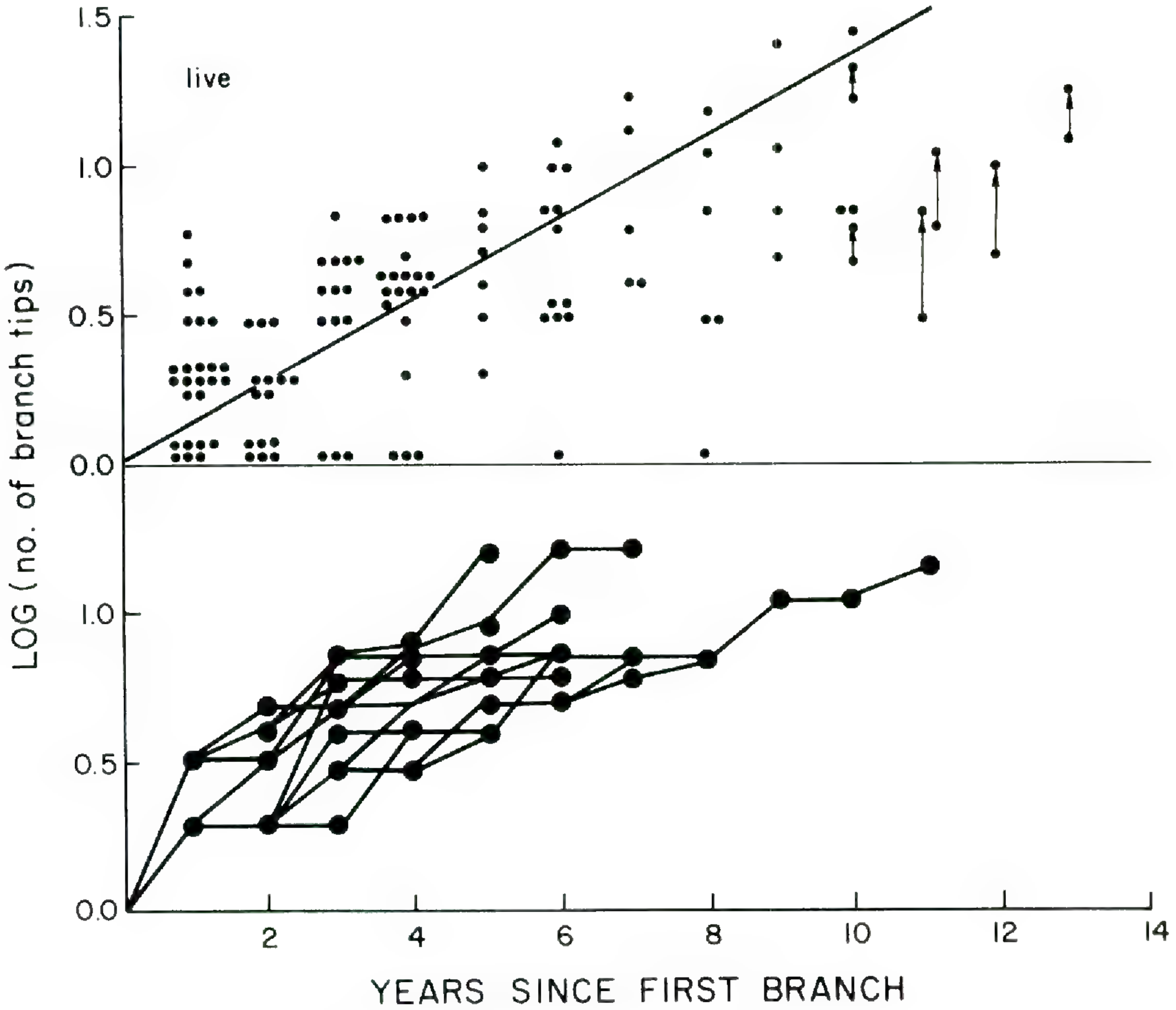


FIGURE 9. Accumulation of live branches (above) and branching trajectories (below) in *Aralia spinosa* as function of number of years since first branching event. Spurs not included. Straight line in upper figure corresponds to model $b = 1.35^x$ (b = number of branch tips, x = ramet age in years). Arrows represent effect of adding dead branches to live ones for selected older ramets (this addition does not take into account any calculated increase in branches if dead branches were alive, flowering and branching). Branching trajectories (lower figure) constructed by superimposing developmental accumulation of branches in all *Aralia* individuals sampled.

of $2^{(\text{age in years})}$ (plants of this species show strict bifurcation every year for the first several years; J. White, 1980). For *Aralia* this early exponential increase of branch number (as determined from regression of the logarithm of branch number on the logarithm of age in years for the first 6 years of branching) approximated $1.35^{(\text{age in years})}$. There was a marked slowing in branch accumulation after this early phase. By age 5, dead branches began to appear in *Aralia* crowns (FIGURE 8, below); these (since they eliminated later branch generations) and the lower number of branches produced per flowering event resulted in a leveling off of branch number after about 10 years. Since the first branching event was so distinctive, the data of FIGURE 8 were recast in FIGURE 9 to show branch accumulation as a function of time after the first branching event. The overall decrease in branch accumulation with age is seen in FIGURE 9 (below), where the individual branching trajectories of all *Aralia* ramets in this data set

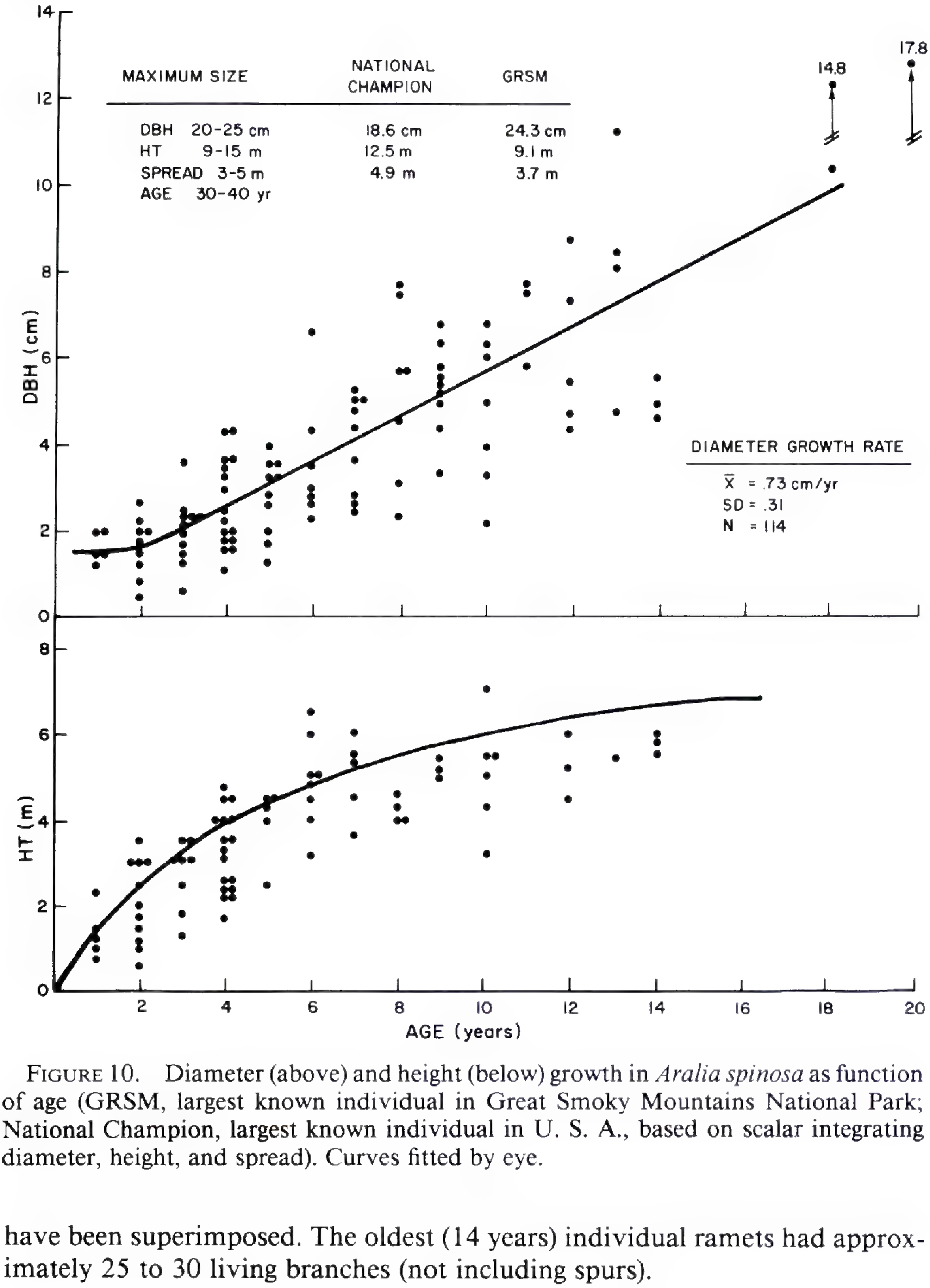


FIGURE 10. Diameter (above) and height (below) growth in *Aralia spinosa* as function of age (GRSM, largest known individual in Great Smoky Mountains National Park; National Champion, largest known individual in U. S. A., based on scalar integrating diameter, height, and spread). Curves fitted by eye.

have been superimposed. The oldest (14 years) individual ramets had approximately 25 to 30 living branches (not including spurs).

BRANCH ANGLES AND CROWN SPREAD

Branch angles (for all orders of branches) averaged 30° when measured between the distal part of the recently terminated axis and the branch base. Because the branch tips curved toward the vertical, the effective branch angle was 5–25° (mean = 15°).

Branched ramets had an overall Y shape, with the crown diameter equal to

77 percent (SD = 52) of crown height (as measured from the first branch). The angle of overall crown spread at the first branch is 42°, giving an effective trunk–to–first-order–branch angle of 21° for each side of the crown—an angle generally larger than that of the higher-order branches.

The shape of the crown as seen from above was determined by the phyllotaxy of nodes (axillary buds) below the first inflorescence and by the number of branches that developed after the first flowering event. The phyllotaxy was 2/5, and the first-order branches were thus separated by 144° on a horizontal plane. The mean number of first-order branches was 2.7. The shape of the crown was initially narrowly elliptic (when two first-order branches developed) to circular (when three first-order branches developed).

Internodal distances increased regularly from the base of each annual increment to its midpoint and then decreased in a similar way to the increment tip. This was true for both fertile and sterile increments, but in the former the upper, more crowded nodes bore the inflorescence branches. The year after flowering, leafy branches developed from axillary buds near the annual increment's midpoint, in the area where the nodes were farthest apart. Together with phyllotaxy, this vertical distance tended to separate the main crown branches.

Bifurcation Ratios

The mean bifurcation ratio was 3.0 if spurs were included and 2.5 if they were not. This ratio was positively and significantly correlated with ramet age ($R = .71$, $P = .05$). In older ramets the bifurcation ratio averaged 4 (spurs included).

Height Growth, Diameter Growth, and Longevity

Aralia grew uniformly in diameter (mean = .73 cm per yr) as it aged (Figure 10, above). However, growth in height slowed (Figure 10, below), with most (ca. 50–60%) occurring in the first 3–4 years (or ca. 10%) of the life span, during the trunk-building phase of growth. Thereafter, extension growth decreased and was no longer concentrated in erect, upward growth. Maximum height in the sampled populations was 7 m; the largest recorded individuals were over 10 m tall (Figure 10). Average height was about 1.5 to 2 times height before flowering. Average stem longevity was ca. 25–30 years; record ages were 40–50 years.

Inflorescence and Fruit Biomass

There was an average of 6360 flowers per inflorescence, with an average total inflorescence weight of 22.5 g, and 905 mature fruits per infructescence, with 5 seeds per fruit (for a total of 4525 seeds per inflorescence). Infructescences averaged 79.4 g dry weight, and their biomass was thus similar in magnitude to total leaf and stem biomass of branch annual increments (ca. 90 g) (note that no estimate was made of the biomass or number of fallen flowers or flower parts). Total biomass (leaves, stems, infructescences) of branch annual incre-

ments was 169.5 g per increment, similar to that of sterile trunk segments (about 200 g per annual increment).

DISCUSSION

The architectural development of *Aralia* ramets was nonstationary (J. White, 1979, 1980; Waller & Steingraeber, in press). In stationary models of growth, the probability of branching and the number of branches produced per branching event are constant. In nonstationary models, the rules of growth vary with time (for example, as a function of plant age or crown development). As long as more than one daughter branch is produced in each branching event, stationary branching results in an exponential increase in branch number over time. Stationary models have been applied to early phases of tree branching and to rhizomatous herbs; in both cases it has been suggested (Waller & Steingraeber, in press) that daughter branches can increase exponentially as long as they do not interfere with one another. Computer simulation of branching in older tree crowns has required the probability of branching to be nonstationary and to decrease as branch order increases (Fisher & Honda, 1977). These simulations produce behavior similar to the logistic model of population growth, with an early exponential increase in branch number followed by a decreasing rate of branching (J. White, 1980; Waller & Steingraeber, in press).

In *Aralia* the number of branches per order decreased as branch order increased. Hence, the rate of branch accumulation in *Aralia* crowns also decreased over time. When compared to higher-order branches, first-order ones also differed in usually remaining sterile for one year (vs. tending to flower the first year), in having greater angles to the parent axis, and in having their points of origin along the parent axis farther apart. Thus the first-order branches are well separated. Among branch orders, the first-order branches are most responsible for the three-dimensional spread of *Aralia* crowns. With the decrease in rate of branch accumulation over time, there was a decrease in height growth rate. Fifty to 60 percent of the total height of *Aralia* shoots was attained during the first three to four years.

The trunk-building and branching phases of growth in *Aralia* differed in ways other than height growth and branching rate. During the trunk-building phase, annual increments were longer, thicker, and heavier (dry weight) than the annual increments of branches. Further, when compared with leaves of branch increments, those of trunk increments were more numerous and longer, with more leaflets and a greater total leaf area. Prickle distribution also differed, with prickles denser on trunk annual increments than on branch annual increments (P. S. White, unpubl. data).

Borchert and Slade (1981) have shown that reduced branch length and reduced rates of branching over time are both necessary to prevent daughter branches from interfering with one another (i.e., in leaf display). Such interference was not measured in the present study; however, data on annual-increment length and branching in *Aralia* lends empirical support to Borchert and Slade's conclusion. A decreasing branching rate was correlated with decreasing length of the annual increments. Decreases in branch length with

increasing branch order have been reported for several tree species (J. White, 1980; Honda, 1971). A decreasing rate of branching over time has been reported for *Acer rubrum* L. (J. White, 1980). Further, decreases in height growth rates over time may be a common property of trees. Site index curves from the forestry literature frequently show a decrease in height growth rate, although the timing of the decrease and the precise shape of the curves vary with species and site quality (see, for example, Trimble & Weitzman, 1956).

Borchert and Slade (1981) also argued that realistic simulations of tree branching require absolute measures of tree morphology (e.g., absolute branch length or leaf size). For example, they predicted that trees with large leaves would experience an earlier decrease in branching rate than trees with small leaves. *Aralia spinosa* has the largest leaves in the arborescent flora of the study area (P. S. White, 1983). The early decrease in branching rate (after the first-order branches developed) is qualitatively compatible with Borchert and Slade's (1981) prediction. A complication in *Aralia* is that leaf size decreases with ramet age. Smaller leaves on the branches decrease branch interference independently of other morphological characteristics.

Bifurcation ratios were nonstationary in *Aralia spinosa.* This has also been reported for *Acer saccharum* Marsh. (Steingraeber *et al.,* 1979), *Lindera benzoin* (L.) Blume (Pickett & Kempf, 1980), and *Populus deltoides* Bartram and *Tabebuia rosea* DC. (Borchert & Slade, 1981). The bifurcation ratio has been criticized as a measure of tree branching because of this nonstationary behavior (Waller & Steingraeber, in press). A second criticism is that the ratio measures only relative attributes of branching (Borchert & Slade, 1981; P. S. White, 1983). For example, *Aralia spinosa* has a bifurcation ratio similar to that of *Acer saccharum* (Whitney, 1976), yet the two species are very different in gross morphology: *Aralia* has larger leaves, has fewer branches at a given leaf area, and displays a given total leaf area in a shorter time than *Acer* (P. S. White, 1983).

Rhus typhina, which also has nonstationary branching and increment length that decreases with increasing branch order (J. White, 1980), is architecturally similar to *Aralia spinosa. Rhus* conforms to Leeuwenberg's architectural model (Hallé *et al.,* 1978). Although *A. spinosa* fits this model better than any other one, Leeuwenberg's model is characterized by two or more branches per module; *Aralia* has only one or two branches per module in all except first-order branches.

Aralia initially accumulated branches at a rate slower than *Rhus.* In addition, *Aralia* remained sterile and in the trunk-building phase for three to four years, while *Rhus* flowers in the first one to two years (Waller, pers. comm.). *Aralia* also continued to produce sterile annual increments in its crowns, whereas *Rhus* shoots usually flower more regularly. The result is that *Aralia* ramets grew taller but accumulated branches more slowly than those of *Rhus.* The comparison of these two relatively simple woody plants suggests that gross morphological traits (size of leaves, number of leaves per annual increment, length of annual increment, rate of branch accumulation, and number of branches) are differently adjusted in different trees, resulting in a range of possible morphological forms within one architectural model (Hallé *et al.,*

1978). The architectural models themselves are based on relative position and development of meristematic tissue (Hallé *et al.,* 1978); like bifurcation ratios, their definition is independent of absolute measures of morphology (e.g., leaf size, annual-increment length, branch-accumulation rates). Differences in gross morphology within architectural models are then to be expected.

In *Aralia,* growth during the trunk-building phase was strongly erect. This phase is keyed to stem establishment. During this period, total leaf area was a function of the number of leaves per annual increment and the amount of leaflet area per leaf. Leaves of the trunk phase differed in both characteristics from those of the branch phase: there were more per increment, and they had a greater total leaflet area. Givnish (1978a, 1978b) has argued that in trees with large leaves, the spread of photosynthetic tissue is partly due to the branched nature of the leaf itself. He predicted that such trees would have fewer woody branches and greater extension growth than smaller-leaved trees. The unbranched phase of growth in *Aralia* lends support to this suggestion. Annual increments during this period of growth were relatively long; however, early successional trees with simple leaves also have long annual increments (Marks, 1975).

In the life history of *Aralia,* the branched phase is also a time of sexual maturity. Fruit production contributed nearly as much late-summer biomass to the annual increments of branches as did first-year stems and leaves. This fruit production may result in a constraint on branching, in addition to the limits imposed by architectural development, as discussed above. Fruit production coincided with decreasing annual-increment length. *Aralia* is short lived; after a tree was in the branched phase ten to twenty years, senescence was marked.

In summary, the life history of *Aralia spinosa* ramets includes a period of unbranched, erect growth (with a high leaf area per increment), a period of first-order branching (with a relatively high rate of branching), and a period of higher-order branching (with a decreasing rate of branch accumulation and frequent flowering). This sequence of events results in nonstationary height growth and branching as a function of ramet age. The three periods are correlated, respectively, with rapid stem establishment, three-dimensional crown spread, and consistent fruit production. This leads to the hypothesis that nonstationary growth in trees is generally a result of trade-offs between the requirement for establishment (i.e., competitive pressure for an early exponential increase in leaf area or branch number) and the branch interference that exponential growth must eventually produce.

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SOME OBSERVATIONS ON THE REPRODUCTIVE BIOLOGY OF THREE SPECIES OF CORNUS (CORNACEAE)

C. V. S. GUNATILLEKE AND I. A. U. N. GUNATILLEKE

SPECIES OF *Cornus* L., commonly known as dogwoods, are ornamental trees or shrubs (rarely herbs) widely cultivated for their handsome inflorescences and showy fruits (Rehder, 1940). The taxonomy, anatomy, embryology, and cytology of *Cornus* species are well documented (Coulter & Evans, 1890; Dermen, 1932; Wilkinson, 1944; Metcalfe & Chalk, 1950; Wilson, 1965; Ferguson, 1966; Goldblatt, 1978). Surprisingly little information is available on their breeding systems, however.

Ferguson (1966), in his treatment of the Cornaceae for the Generic Flora of the Southeastern United States, mentioned that pollination in *Cornus* is probably by insects, including small creeping Coleoptera and some Diptera and Hymenoptera. He also speculated that cross-pollination is promoted by the difference in style and stamen length, but that self-pollination may occur when the stamens spread and touch neighboring flowers.

Because no substantiating experimental evidence was available on the nature of the breeding systems in this genus, controlled pollination experiments were performed on three species of *Cornus* using plants cultivated at the Case Estates of the Arnold Arboretum, Weston, Massachusetts. These species were *C. florida* L. (flowering dogwood), native to eastern North America and an understory tree in mixed deciduous forests; *C. sericea* L. (red-osier dogwood), found along the Atlantic and Pacific coasts of North America, and a widespread shrub common on river banks and in wet thickets; and *C. mas* L. (cornelian cherry), native to central and southern Europe and introduced into the United States before 1800. It is a small understory tree in oak forests in its native habitat (Rehder, 1940; Seymour, 1969).

MATERIALS AND METHODS

Two individuals each of *Cornus florida* (Arnold Arboretum accession nos. 272-51A and 272-51B) and *C. sericea* (843-69A and 843-69B) and three of *C. mas* (422-67, 424-67A, 424-67B), all growing at the Case Estates, were used for experimentation. Records maintained at the Arnold Arboretum (Case Estates Nursery Catalogue, 1981) indicate that plants of the latter two species were raised from seed, while those of *C. florida* were grafts of a small-flowered form received from the Morris Arboretum in Philadelphia; none of them is a horticultural variety.

The pollination experiments carried out included the following treatments:

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1a. Flowers emasculated and bagged only, to prevent pollen from reaching the stigma of the enclosed flowers. Any fruit set observed in this treatment would indirectly indicate agamospermy or apomixis.

1b. Flowers emasculated, selfed, and bagged. Mature flowers were hand-pollinated using pollen from different flowers obtained from the same plant. Comparison of fruit set here with that of 1a would indicate capacity for self-fertilization.

1c. Flowers emasculated, crossed, and bagged. Mature flowers were hand-pollinated using pollen from another individual (with a different genotype) of the same species. Any fruit set here would indicate the capacity for outcrossing.

1d. Flowers emasculated and left open without bagging, to determine whether emasculation adversely affects fruit set. No hand-pollination was done, and any fruit set here would be the result of natural pollination.

The same treatments were repeated using nonemasculated flowers (2a–d) in order to compare the results of the two methods employed (i.e., manipulation of emasculated and nonemasculated flowers), both of which have been widely used in studying breeding systems (Bawa, 1974; Chan, 1981).

Bagging and/or emasculation were done at the mature-bud stage, before the flowers opened or the anthers dehisced. Pollen used in pollination was collected from previously bagged flowers so that pollen contamination by insect visitors, wind, or even water was avoided as far as possible. For details of bagging, see Chan (1977). Hand-pollination was accomplished by brushing stigmas of experimental flowers with mature, dehisced anthers containing pollen. This was done on three consecutive days for each treatment, and at different times each day, to insure pollination when the stigma was receptive. Each treatment was done on at least two separate branches of each plant. For treatments in which flowers were enclosed, the bags were removed once the flowers withered and early stages of fruit set were evident. The numbers of flowers pollinated and of fruits and seeds set were recorded for each treatment of each individual.

Pollen-tube germination on the stigma and style was also examined in five to ten flowers each from treatments 1a, 1b, and 1c collected 24, 48, and 72 hours after hand-pollination. The gynoecium of each of these flowers was dissected out and fixed in a mixture of formaldehyde, glacial acetic acid, and ethyl alcohol (2:1:10) as described by Sass (1958). These were cleared in 8 M NaOH, stained with 1 mg/ml aqueous aniline blue in a 0.15 M solution of K_3PO_4, squashed, and examined under a fluorescence microscope (for details of the procedure, see Martin, 1959).

The phenology of flowering and fruiting of these species, as well as the diurnal visitors during the flowering period, was also recorded.

RESULTS

INFLORESCENCE STRUCTURE

In the three species studied, flowers are borne in inflorescences: umbels in *Cornus mas*, globose heads (condensed cymes) in *C. florida*, and lax cymes in

TABLE 1. **A summary of floral and fruit characters of three species of Cornus.**

CHARACTER	SPECIES		
	Cornus mas	*Cornus florida*	*Cornus sericea*
Inflorescences			
Type	Umbel	Head (condensed cyme)	Compound cyme
Diameter (mm)	20	80–100	40–70
Length of peduncle (mm)	2–3	30–35	24–45 (1st-order stalk) 17–20 (2nd-order stalk) 10–12 (3rd-order stalk)
Flowers			
Number per inflorescence	16 to 34	15 to 35	75
Length of bracts (mm)	6–7	27–30	(Absent ?)
Length of pedicel (mm)	10	(Flowers sessile)	2–4
Calyx	Green, inconspicuous	Green, accrescent, persistent in fruit	Green, inconspicuous
Corolla	Yellow	White	White
Color of nectary	Cream, turning dark brown	Cream, turning dark brown	White, turning light brown, then scarlet
Scent	Strong, unpleasant	Absent	Absent
Fruits			
Position relative to leaves at maturity	Hanging vertically downward, below leaves	Upright, above leaves	Upright, above leaves
Length of stalk (mm)	15–17	(Fruits sessile)	2–4
Bracts	Persistent	Deciduous	Absent
Size at maturity (mm)	15–17 × 9–10	10 × 6	8 × 8
Color at maturity	Red	Red	White
Size (mm) and shape of seeds	14 × 7, elliptic	10 × 4, elliptic	7 × 4, globose to oval

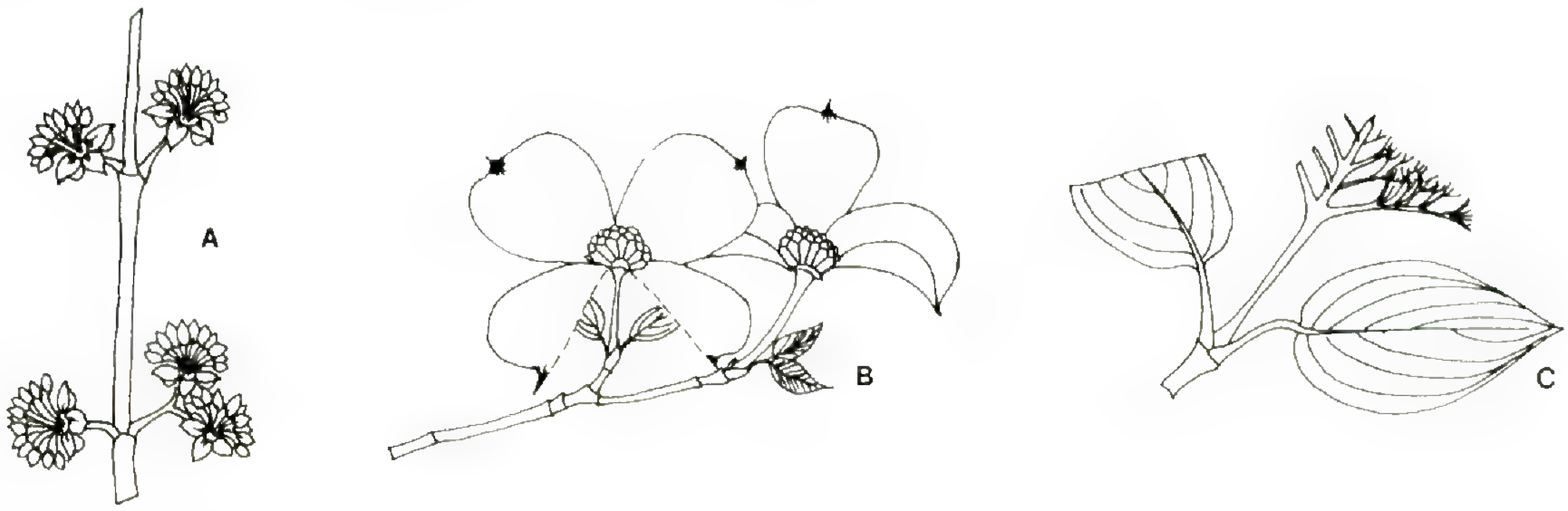

FIGURE 1. Inflorescence types and stages of foliar development at time of bloom, × 0.3: A, *Cornus mas*; B, *C. florida*; C, *C. sericea*.

C. sericea. The species have been described by Rehder (1940) and by Fosberg (1942). Some differences in the structure of their inflorescences appear to be related to their pollination biology (see FIGURE 1, TABLE 1, and discussion).

PHENOLOGICAL OBSERVATIONS

Cornus mas commenced blooming as early as March 25, 1983, in our experimental plants. In this species the maximum number of flowers open at any given time was observed two weeks after initial bloom, and flowering was complete around the end of April. *Cornus florida* and *C. sericea*, on the other hand, bloomed only in May and showed an overlap in their flowering periods (FIGURE 2). Duration of bloom was about five to six weeks in *C. mas* and *C. florida*, and about four weeks in *C. sericea*. Longevity of individual flowers (the time period between opening and withering of the corolla) was about six to eight days in the two former species, and four or five days in the latter one.

In *Cornus mas* and *C. sericea* anther dehiscence followed opening of the flowers, while in *C. florida* it occurred in mature buds just before flower opening. In all species the corolla and stamens were deciduous after anthesis.

Differences in the size of ovaries with fertilized and unfertilized (or aborted) ovules were evident only about six to seven weeks after pollination in *Cornus mas* and four weeks after in *C. florida*. In both of these species, all ovaries remained green. In *C. sericea*, however, not only was the size difference distinguishable within three weeks, but the unfertilized or aborting ovaries turned purplish red. In *C. mas* the ovaries that failed to set seed were shed long before the successful ones were fully mature. In the other two species they remained on the plant but without any appreciable increase in size right up until fruit maturity, at which time they, too, were shed.

Fruits of *Cornus sericea* ripened, turning white as early as mid-July, and were shed soon thereafter. In contrast, fruits of *C. mas* began to ripen in August, and by late August the pericarps were fleshy, shiny, and bright red. At this time fruits of *C. florida* were still green, and the undeveloped, smaller ovaries were yet unshed; the disparity in their sizes was, however, quite evident.

In these three *Cornus* species, buds that would function as flowers or foliage the following year (i.e., 1984) were already evident by early August of 1983.

TABLE 2. **Percentage of fruit set after different pollination treatments in three species of Cornus.**

TREATMENT	SPECIES					
	Cornus mas (3)*		*Cornus sericea* (2)*		*Cornus florida* (2)*	
	No. of flowers treated	**Fruit set (%)**	**No. of flowers treated**	**Fruit set (%)**	**No. of flowers treated**	**Fruit set (%)**
1a. Emasculated and bagged	238	3	222	2	245	0
2a. Nonemasculated and bagged	381	1	200	0	279	1
1b. Emasculated, selfed, and bagged	320	0	187	3	325	0
2b. Nonemasculated, selfed, and bagged	524	2	281	1	293	0
1c. Emasculated, crossed, and bagged	622	21	234	44	309	28
2c. Nonemasculated, crossed, and bagged	695	11	251	36	281	17
1d. Emasculated and open-pollinated	287	5	205	34	357	2
2d. Nonemasculated and open-pollinated	756	13	266	35	312	5

*The total number of plants studied for each species.

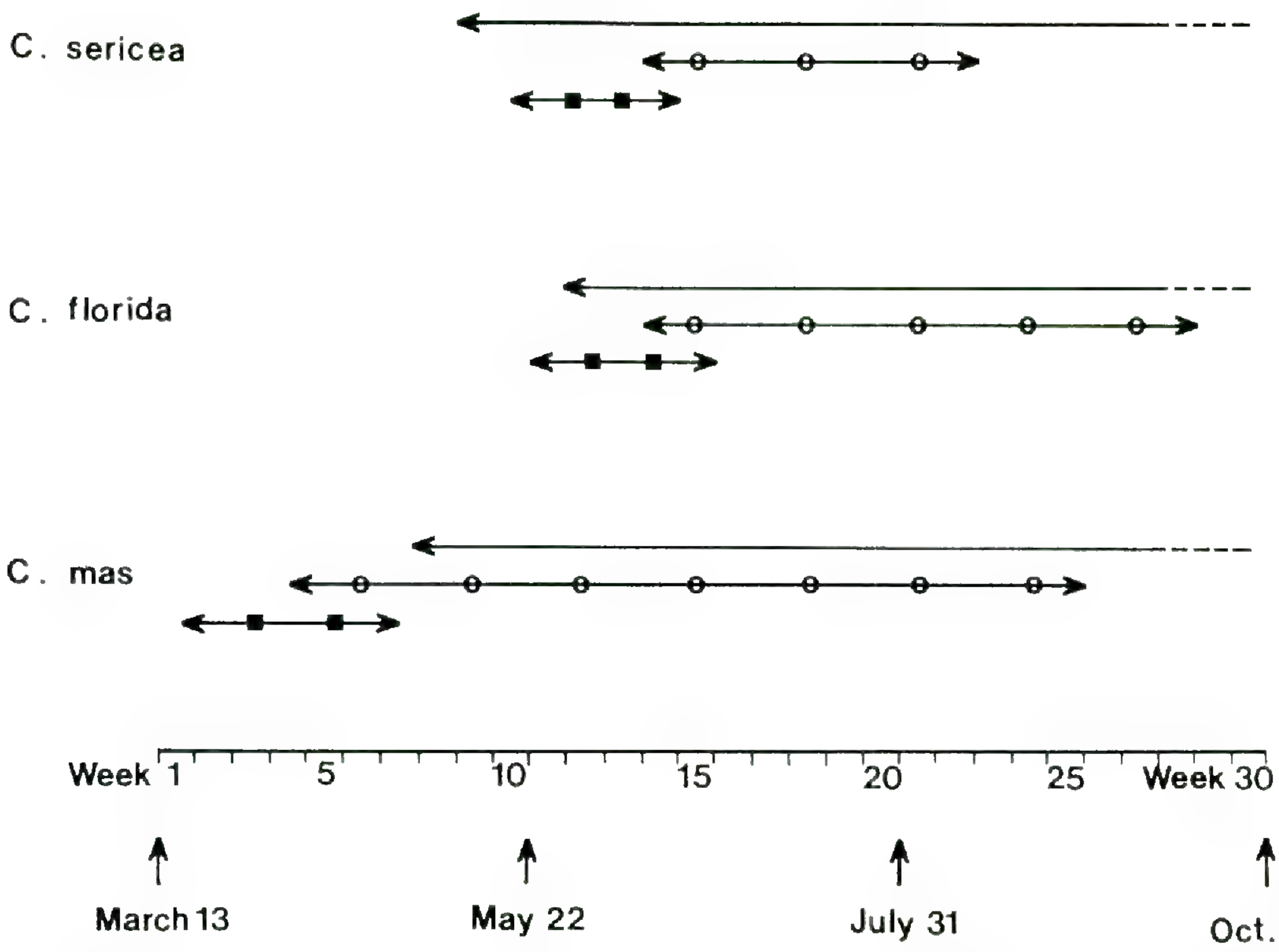

FIGURE 2. Duration of bloom (lines with squares), fruit development (lines with circles), and foliage (solid lines) in *Cornus* spp. at Case Estates of Arnold Arboretum, March–September, 1983. (Plants still in foliage, dashed line.)

When dissected and examined under the light microscope, the buds of *C. mas* and *C. florida* that were externally visible in late August were found to be flower buds; the identity—vegetative or reproductive—of those of *C. sericea* could not yet be discerned. These buds of *Cornus* species develop up to a point during the summer, remain dormant through the winter, and expand (or complete development) with the advent of favorable conditions the following spring to carry out their respective functions the second year.

INSECT VISITORS

The most commonly observed insect visitors on the species of *Cornus* studied were the honey bee (*Apis mellifera*) and the bumble bee (*Bombus* sp.). A third type of bee, *Andrena* sp., also visited *Cornus mas* and particularly *C. sericea.* Unlike the honey bee and the bumble bee, which appeared to forage mostly on pollen of these species and remained only a few seconds on each flower, individuals of *Andrena* sp. spent 20–40 seconds on each flower and possibly fed on the nectar. The fly species *Epalpus signifer* and *Pollenia rudis* were also seen on *C. mas,* but they appeared to be disinterested in either nectar or pollen and were probably casual visitors rather than foragers on this species. For insect visitors to dogwood flowers other than those reported here, see Knuth (1898), Robertson (1928), LaBerge and Ribble (1972), and Maier and Waldbauer (1979a, 1979b).

Breeding Experiments

Results of the pollination experiments are summarized in Table 2. In all three species of *Cornus* studied, fruit set in emasculated or nonemasculated, bagged flowers (1a and 2a, respectively), as well as emasculated or nonemasculated, selfed and bagged flowers (1b and 2b, respectively), was extremely low ($\leq$ 3%). By contrast, plants that were cross-pollinated (1c and 2c) yielded a fruit set of 11–44 percent, depending on the species. Fruit set in *C. sericea* was higher than that in the other two species in both cross- and open-pollination experiments (see Table 2). In open-pollinated plants (1d and 2d) nonemasculated flowers set more fruit than emasculated ones in both *C. mas* and *C. florida* but an almost equal percentage in *C. sericea.* However, in cross-pollinated flowers of all three species, the emasculated flowers yielded a higher fruit set than the nonemasculated ones. In all but one instance (*C. mas*, 2c), cross-pollinated and bagged flowers had a higher percentage of fruit set than open-pollinated ones.

In both self- and cross-pollinated flowers of all three species, pollen grains germinated on the stigmatic surface and grew through the stylar tissue. Growth was slower in the selfed flowers than in those that were crossed, however.

DISCUSSION

The different inflorescence types of *Cornus mas, C. florida,* and *C. sericea* appear to be related to the phenology of leaf production and to adaptations for pollination success. In *C. mas* flowering precedes leaf emergence. Consequently, the small, short-peduncled umbels are fully exposed to visiting insects. In *C. florida* the foliage begins to appear after flowering has commenced but before it is completed. The enlarged, showy bracts of the inflorescence heads in this species, together with their relatively long peduncles, are probably its adaptations for effective pollination. By contrast, in *C. sericea* leaves are formed well in advance of flower production. Here the compound cyme has not only a much larger diameter and many more flowers per inflorescence than the other two species, but also a relatively long peduncle that lifts the pollination unit well above the leaves.

Although *Cornus sericea* came into flower last of the three species studied, it completed its fruiting cycle much sooner than the others. One of the factors contributing to its rapid fruit set could be the early growth of foliage prior to flowering and fruiting, which possibly enables the species to provide adequate food resources to the developing fruit soon after fertilization. In *C. mas* leaves emerged only several weeks after young fruits had formed. An intermediate situation appears to prevail in *C. florida.*

These observations also give us some insight, little though it may be, into the resource partitioning in these species. It could be speculated that in *C. mas* and *C. florida* the previous year's photosynthetic products provide the resources necessary for the current year's floral and foliar expansion, whereas in *C. sericea* the previous year's resources appear to suffice only for the current year's foliage production. In this species resources necessary for flowering presumably come

from the current year's photosynthetic products. In all three species resources for fruit development may be provided by the current year's growth. These differences in resource partitioning may also be related to growth habit in the species studied; *C. mas* and *C. florida* are both small trees, while *C. sericea* is a shrub.

Results of controlled pollination experiments performed in this study imply several conclusions. First, the three species examined are self-incompatible, and out-crossing is obligate. Self-sterility in dogwoods, including *Cornus mas,* has also been previously reported (D'Amato, 1947; Hummel *et al.,* 1982; Ohta, 1971). The very low percentage of fruit set in self-pollinated flowers is probably due to contamination during floral manipulation. Second, the low fruit set in emasculated and bagged flowers, which again may be due to contamination, provides indirect evidence for the absence of agamospermy or apomixis. Further, because fruit set in nonemasculated and bagged—as well as selfed and bagged—flowers is ca. 3 percent or less, we infer that self pollen on the stigma does not stimulate or trigger agamospermy in these species. Third, microscopic observations of pollen-tube germination in stylar tissue of selfed flowers suggest that the self-incompatibility barrier in these species operates beyond the stigmatic surface. It also rules out nonviability or germination deficiency of selfed pollen as an explanation for lack of self-fertilization. The observation that ovaries (or young fruits?) of self-pollinated flowers remain a long time on the parent plant before they are ultimately shed suggests the operation of a postzygotic barrier to self-incompatibility. However, only embryological studies will confirm whether this incompatibility is pre- or postzygotic. Fourth, the greater percentage of fruit set in emasculated and cross-pollinated flowers as compared to nonemasculated and crossed ones suggests that in nonemasculated flowers self pollen competes for space on the stigma and possibly thus contributes to lower fruit set. Fifth, the low fruit set in open-pollinated plants of *C. florida* is attributable to the absence of other genetically different individuals of this species within a radius of about 60 m of the two experimental trees, whose origin may be traced back to grafts. Sixth, although *C. mas* has been introduced into North America from central and southern Europe, its reproductive success—judged by fruit and seed set in open-pollinated flowers—indicates that local pollinators are quite effective in cross-pollinating this species. The extent to which wind contributes to pollination was not investigated in this study.

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SYSTEMATICS OF CENTRAL AMERICAN HELICONIA (HELICONIACEAE) WITH PENDENT INFLORESCENCES[1]

W. JOHN KRESS

THE FIRST botanical description of *Heliconia* was by Plumier in his *Nova Plantarum Americanarum Genera* (1703). He provided a short generic description of the genus *Bihai* and polynomials for three taxa: *Bihai amplissimis foliis, florum vasculis coccineis*; *Bihai amplissimis foliis, florum vasculis subnigris*; and *Bihai amplissimis foliis, florum vasculis variegatis.*

In his *Species Plantarum* (1753), Linnaeus included these three taxa in a single species, *Musa bihai,* retaining Plumier's exact diagnoses and placing the "variegatis" variety first. Miller (1754, 1768) and Adanson (1763) considered these plants generically distinct from other species of *Musa* and used the generic name *Bihai.* In *Mantissa Plantarum* (1771), Linnaeus also segregated *M. bihai* into its own genus, *Heliconia* L. He provided a generic description of *Heliconia* and gave a short diagnosis of a species, *H. bihai,* with red cincinnal bracts and yellow flowers. Kuntze (1891; substituting the variant spelling *Bihaia*) and later Griggs (1904, 1915) recognized the earlier generic name and transferred all species of *Heliconia* known to them into *Bihai* Adanson. However, at the International Botanical Congress held in Vienna in 1905, *Heliconia* was reinstated as a *nomen conservandum* (Farr *et al.,* 1979).

Around the turn of the century, a number of workers attempted revisions or summaries of the genus. Petersen (1890) and Kuntze (1891) each listed 25 species. Baker (1893), the first to provide an infrageneric classification of the genus, supplied descriptions and keys for 29 species. In 1900 Schumann summarized the genus for Engler's *Das Pflanzenreich* but added no new species and simply translated abbreviated versions of Baker's earlier descriptions into Latin. Griggs was one of the most knowledgeable students of *Heliconia,* due

[1]A part of a thesis (Kress, 1981b) submitted to the Department of Botany, Duke University, in partial fulfillment of the requirements for the Ph.D. degree.

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in part to his study of plants in the field. However, he never produced a thorough revision, although he did publish several papers on the genus (1903, 1904, 1915). The last of these papers recognized 48 Neotropical species and contained an infrageneric classification that was more detailed than the one proposed by Baker in 1893.

Since the treatment by Griggs in 1915, there has been no major revision of the genus in its entirety. During the last 65 years, many new species have been described and several regional floristic treatments have added to our knowledge of the variation and diversity within *Heliconia*. Lane began work on the genus at Harvard University in the late 1940's and annotated many herbarium specimens with names of new species and varieties, but unfortunately he never published any of these taxa. Recently, Andersson (1981) has provided a modern revision of the species related to *H. bihai* (sect. HELICONIA) that is based primarily on herbarium material and has solved many of the taxonomic and nomenclatural problems of that group. Floristic treatments are available for the heliconias of Guatemala (Standley & Steyermark, 1952), Costa Rica (Standley, 1937), Panama (Woodson & Schery, 1945), Middle America (Smith, 1968), Venezuela (Aristeguieta, 1961), Peru (Macbride, 1936), and the Old World (Green, 1969), but most of the studies are now out of date and incomplete. Recent workers in Costa Rica (Daniels & Stiles, 1979), Nicaragua (Smith, 1977, 1980), Panama (Kress, 1981a), Colombia (Abalo & Morales, 1982, 1983b), Ecuador (Dodson & Gentry, 1978; Abalo & Morales, 1983a), and Brazil (Barreiros, 1971, 1976, 1978; Emygdio, 1975, 1976; Santos, 1978) have described many new species. The work of Daniels and Stiles (1979) in particular is an excellent example of the importance of field work in understanding taxonomic delimitations within *Heliconia*.

INFRAGENERIC CLASSIFICATION

Several infrageneric classifications of *Heliconia* have been proposed (see TABLE 1), each one more complex and composed of more hierarchical ranks than its predecessor. Early authors based their groups solely on the shape of the cincinnal bracts. Later workers also used plant size, leaf orientation, and inflorescence habit and structure to devise more detailed—and supposedly more natural—classifications.

Kuntze (1891) published the first infrageneric taxon above the rank of species. The two species contained within sect. *Taeniostrobus* Kuntze—*Heliconia imbricata* and *H. mariae*—are characterized by imbricate cincinnal bracts. Baker (1893, p. 190) divided the genus into two subgenera, *Platychlamys* Baker and *Stenochlamys* Baker, the former containing all species with "ovate-acuminate, deeply boat-shaped" cincinnal bracts; the latter, species characterized by bracts that are "lanceolate-acuminate, shallowly boat-shaped." Schumann (1900) followed Baker's classification except that he placed *Platychlamys* in synonymy under *Taeniostrobus* and altered the ranks of these taxa from subgenera to sections.

Griggs's superior knowledge of the genus was reflected in his more complete and less artificial classification. He recognized (1903, p. 644) that infrageneric

TABLE 1. **History of the infrageneric classification of Heliconia.**

BAKER (1893)	SCHUMANN (1900)	GRIGGS (1903)	GRIGGS (1915)*
Subg. *Platychlamys* Baker	Sect. *Taeniostrobus* Kuntze	Subg. *Taeniostrobus* Kuntze	Subg. *Taeniostrobus* Kuntze *Episcopales* Griggs *Imbricatae* Griggs *Champneianae* Griggs *Pendulae* Griggs
Subg. *Stenochlamys* Baker	Sect. *Stenochlamys* Baker	Subg. *Platychlamys* Baker	
		Subg. *Stenochlamys* Baker	Subg. *Stenochlamys* Baker *Distantes* Griggs *Cannoideae* Griggs

*Under the generic name *Bihai*.

groups based upon a single character, cincinnal bract shape, inadequately expressed species relationships: "It is not to be denied that the shape of the branch-bracts [cincinnal bracts] is in a general way correlated with the relationships of the species, but it is only an accidental parallelism without much physiological importance, for there are many exceptions—species quite similar in all respects except that the branch-bracts are sufficiently different to place them in different subgenera. . . ." In a diagnostic key he included three subgenera, *Stenochlamys, Platychlamys,* and *Taeniostrobus,* defined by plant habit and cincinnal-bract orientation.

Griggs later (1915) replaced this classification with one consisting of two subgenera (*Taeniostrobus* and *Stenochlamys*) and six subordinate taxa of unspecified rank. All species known at that time were included in his treatment. Plant habit and height, inflorescence orientation, and distance between adjacent cincinnal bracts were characters used to recognize subgeneric groups. However, the actual phylogenetic relationships within *Heliconia* are much more complex than is represented in Griggs's final classification.

Some question exists as to whether Griggs formally proposed the six subordinate taxa in his 1915 publication because he did not specify their rank. The International Code of Botanical Nomenclature (Stafleu, 1978) specifies that a new name published before 1953 does not require clear indication of rank. In addition, although no formal descriptions or diagnoses were provided, the taxa were sufficiently differentiated in the key provided by Griggs in the same publication. The names for the infrageneric taxa comply with all the other requirements of the Code for valid publication at that time. Griggs's infrageneric names must therefore be recognized as validly published but without indicated rank.

In the present treatment, I do not propose any new classification of *Heliconia.* Rather, I have purposefully chosen to study in depth a group of species—those with pendent inflorescences—that has previously been classified as a natural assemblage. Where possible, these species are compared with others not included in this taxonomic group. In addition to broad morphological compar-

isons, I have used information on breeding systems, results from artificial and natural interspecific hybridization, and analyses of pollen structure to assess the phylogenetic status of the assemblage. The information provided here will hopefully establish a foundation upon which a more natural classification of the entire genus can eventually be constructed.

Griggs (1903, 1915) was the first to suggest that species of *Heliconia* with pendent inflorescences are closely interrelated, and he included most of these species in his unranked *Pendulae*. However, by placing several species that he described as having pendent inflorescences (*H. punicea, H. mariae,* and *H. curtispatha*) into a group characterized by erect inflorescences (*Imbricatae*), he indicated that inflorescence habit was not necessarily an indication of close relationship.

The present revision includes all Mexican and Central American taxa of *Heliconia* with pendent inflorescences (there are no known species with pendent inflorescences in the Antilles). The nineteen species and eight varieties involved fall into three of Griggs's lower groups, *Imbricatae, Pendulae,* and *Distantes.* One object of this study was to test the hypothesis that the pendent inflorescence habit is a uniquely derived state in the genus that characterizes a monophyletic group of species. Ideally, all pendent species, including those from South America, should have been incorporated into the study. Unfortunately, a total revision was not logistically possible due to the large number of species, the wide geographic distribution, and the extensive field work needed to investigate the group adequately. For this reason the conclusions reached here concerning the *Pendulae* can only underestimate the complexity of this infrageneric group. Because of this complexity and our lack of knowledge, it is still premature to assign any rank to Griggs's *Pendulae.* A final statement on the phylogenetic classification of *Heliconia* must await a treatment of the entire genus. An extension of the present revision of the Central American species with pendent inflorescences to include the South American species (approximately 50) is planned.

THE HELICONIACEAE

The proper classification of the order Zingiberales has been debated since 1880, when Bentham and Hooker first established four tribes within the Scitamineae. Subsequent authors have subdivided and altered the rank of each of the original four tribes (see TABLE 2). Most current workers recognize eight families within the order.

Heliconia has always been allied with the *Musa* complex that includes *Orchidantha* N. E. Br., *Musa* L., *Ensete* Horan., *Strelitzia* Banks, *Ravenala* Adanson, and *Phenakospermum* Endl. These genera are recognized as distinct from other members of the Zingiberales by their usually arborescent habit and their flowers with five (or six) pollen-bearing stamens. Lane (1955) presented convincing evidence for segregating *Orchidantha* into a monotypic family, the Lowiaceae (proposed by Hutchinson, 1934). He retained the remaining genera in a single subdivided family, the Musaceae. Subdivision of the family into several ranks, Lane believed, best shows the relationships of the genera. He

TABLE 2. **Systems of classification.***

BENTHAM & HOOKER (1880) Order: Scitamineae	ENGLER & PRANTL (1889) No rank	ENGLER (1900, 1902, 1904, 1912) Order: Scitamineae	ENGLER & PRANTL (1930) Order: Scitamineae	HUTCHINSON (1934, 1959) Order: Scitamineae	NAKAI (1941) TOMLINSON (1962) CRONQUIST (1981) DAHLGREN & CLIFFORD (1982) Order: Zingiberales
Tribes	Families	Families	Families	Families	Families
Zingibereae	Zingiberaceae	Zingiberaceae Subfamilies Zingiberoideae	Zingiberaceae Subfamilies Zingiberoideae	Zingiberaceae Tribes Zingibereae Hedychieae Globbeae	Zingiberaceae
		Costoideae	Costoideae	Costeae	Costaceae
Maranteae	Marantaceae	Marantaceae	Marantaceae	Marantaceae	Marantaceae
Canneae	Cannaceae	Cannaceae	Cannaceae	Cannaceae	Cannaceae
Museae (*Musa, Ravenala, Strelitzia, Heliconia*)	Musaceae Tribes Museae (*Musa, Ravenala, Strelitzia*)	Musaceae Subfamilies Musoideae (*Musa*)	Musaceae Subfamilies Musoideae (*Musa*)	Musaceae (*Musa*)	Musaceae (*Musa, Ensete*)
		Strelitzioideae Tribes Strelitzieae (*Strelitzia, Ravenala*)	Strelitzioideae Tribes Strelitzieae (*Strelitzia, Ravenala*)	Strelitziaceae (*Strelitzia, Ravenala, Phenakospermum, Heliconia*)	Strelitziaceae (*Strelitzia, Ravenala, Phenakospermum*)
	Heliconieae (*Heliconia*)	Heliconieae (*Heliconia*)	Heliconieae (*Heliconia*)		Heliconiaceae (*Heliconia*)
		Lowioideae	Lowioideae	Lowiaceae	Lowiaceae

*After Tomlinson (1962).

argued that *Heliconia* is the most divergent genus, more closely allied to *Musa* than to the other three genera. After extensive anatomical studies of the order, Tomlinson (1962) concluded that all eight divisions of the Zingiberales exhibit about the same degree of morphological and anatomical differentiation, and that each should be regarded as a family. He therefore followed the suggestion of Nakai (1941) and recognized the Heliconiaceae (including only *Heliconia*) and the Strelitziaceae (comprising *Strelitzia, Ravenala,* and *Phenakospermum*) as distinct from the Musaceae (containing *Musa* and *Ensete*). Recent studies on pollen of the Zingiberales (Kress *et al.,* 1978; Stone *et al.,* 1979, 1981) support Tomlinson's morphological and anatomical evidence for the recognition of the Heliconiaceae, and his classification is accepted here. Other recent authors (Stebbins, 1974; Takhtajan, 1980; Cronquist, 1981; Dahlgren & Clifford, 1982) have also adopted this classification.

MORPHOLOGY

The distinctive morphology of members of the genus *Heliconia* merits a short descriptive summary. The following descriptions are taken from observations of living plants and in some cases are not readily applicable to dried herbarium specimens. Although not all character states discussed (e.g., shoot habit, leaf venation, pedicel twisting) are applicable to species with pendent inflorescences, they are nonetheless included to facilitate comparison with other species and to aid workers unfamiliar with the genus.

LIFE FORM

The genus comprises medium to large erect herbs often with extensive sympodial rhizomatous growth (Bell & Tomlinson, 1980). The patterns of production of rhizomes, rhizomatous branches, and erect shoots result in varying capacities for vegetative colonization and differ among species. An investigation of interspecific variation in rhizome morphology and branching pattern may yield information of taxonomic value. Each erect shoot is composed of a pseudostem and leaves, and it is often—although not always—terminated by an inflorescence (FIGURE 1). The pseudostem is made up of an axis covered by overlapping sheathing leaf bases, can be up to several meters in length, and has various colors and textures. In some species (e.g., *Heliconia platystachys*) the pseudostem has a distinctive white, waxy bloom.

LEAVES

Leaf arrangement is distichous. If the leaves are oriented vertically and have long petioles, the plants have the aspect of a banana plant and are called "*Musa*-like" (FIGURE 1, A). If the leaves are more or less horizontally positioned and the blades are short petiolate or essentially sessile on the pseudostem, the plants have the aspect of a ginger plant and are called "*Zingiber*-like" (FIGURE 1, C). These terms correspond to the somewhat confusing terms "musoid" and "cannoid," respectively, of other authors (Schumann, 1900; Griggs, 1915; Smith,

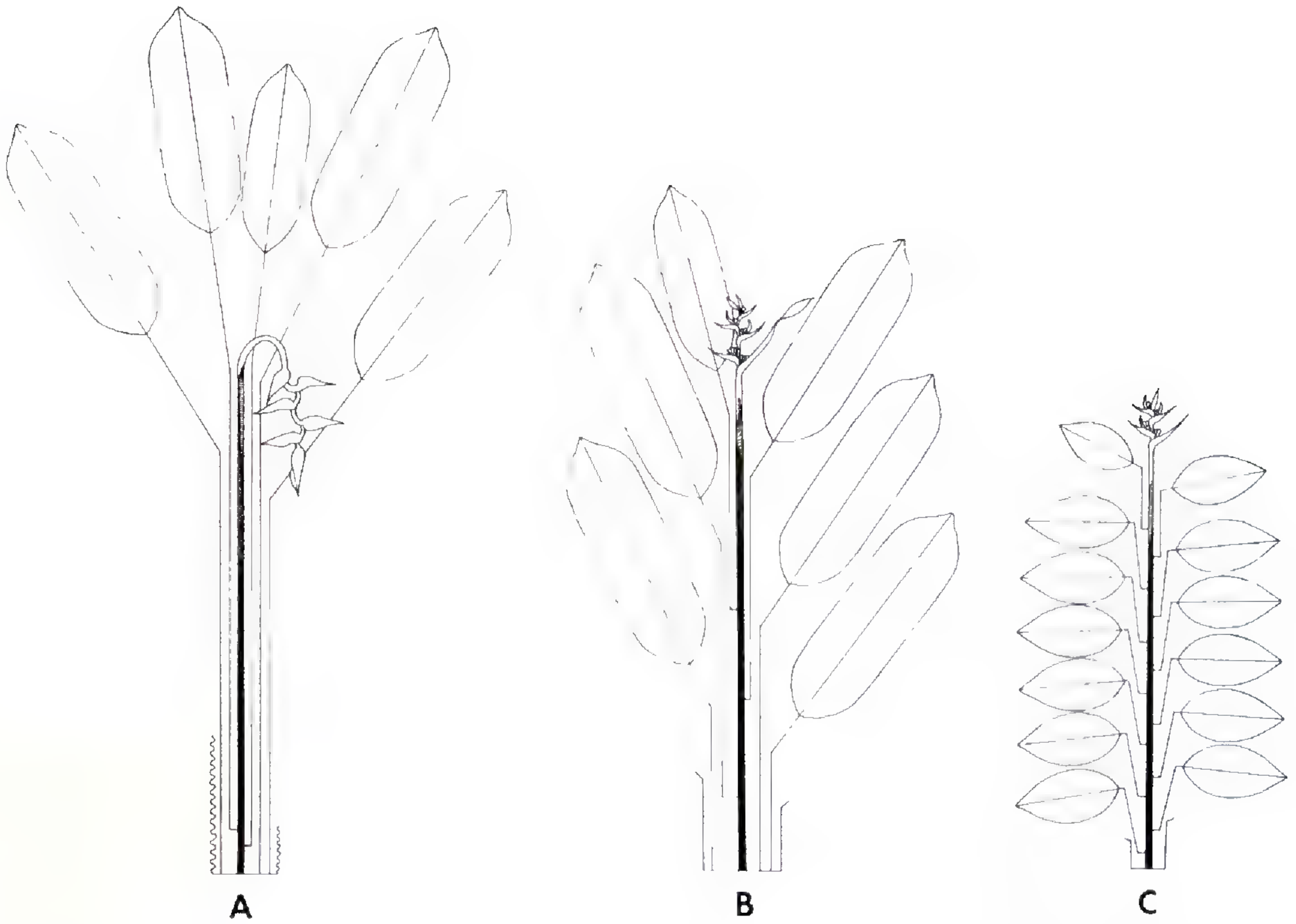


FIGURE 1. Schematic representation of the 3 types of shoot organization in *Heliconia*: A, *Musa*-like; B, *Canna*-like; C, *Zingiber*-like.

1968; Daniels & Stiles, 1979; Andersson, 1981; Abalo & Morales, 1982, 1983a). Some species may have short or medium-length petioles with blades that are held obliquely, and they indeed have a shoot organization resembling that in species of *Canna*. Such plants are called "*Canna*-like" (FIGURE 1, B). The leaves of a single shoot in *Zingiber*-like species usually lie in a single plane. This same planar configuration is characteristic of some *Musa*-like species (e.g., *Heliconia maculata, H. trichocarpa*) whose leaves often fan out from stream banks or from the slopes of small embankments.

Lateral veins run perpendicular or oblique to the central midrib (Tomlinson, 1959). Abaxial venation, although usually green and obscure, is sometimes distinctive in color (e.g., in *Heliconia reticulata*), and the midrib usually differs from the lamina in color and texture both adaxially and abaxially.

The lamina is usually green, but in some species (e.g., *Heliconia ramonensis, H. secunda* var. *viridiflora*) it is often tinted maroon or red abaxially, especially along the margin. In most species it is elliptic-oblong, coriaceous, entire, and glabrous adaxially and abaxially. Notable exceptions are oblanceolate blades (in the *trichocarpa* group), those that split into narrow lateral segments with age (e.g., in *H. magnifica*), and those having a thick, white, waxy bloom abaxially (e.g., *H. curtispatha, H. collinsiana* var. *collinsiana*). The apex is acute to acuminate, and the base is nearly always unequal, with one side extending farther along the petiole. In most cases the base is obtuse to truncate, but it can be cordate, or even attenuate along the petiole (e.g., in *H. maculata*).

INFLORESCENCES

Inflorescences are almost always terminal on erect, leafy shoots, but in a few species (e.g., *Heliconia metallica*) they may arise on a basal leafless shoot. When terminal, the inflorescence may have an erect or pendent orientation with respect to the leafy shoot from which it emerges (FIGURE 1). In some taxa (e.g., *H. secunda, H. sessilis,* and some hybrids between erect and pendent species) the inflorescence is carried in an intermediate, nodding posture. The peduncle (the part of the stem between the terminal leaf sheath and the basal cincinnal bract; FIGURE 2, A) may have various colors and textures. The inflorescence is made up of modified leaflike structures called cincinnal bracts ("branch-bracts" or "spathes" of previous authors), the rachis connecting adjacent cincinnal bracts, and a cincinnus of flowers within each bract. Measurements of inflorescence length do not include the peduncle. The rachis (FIGURE 2, B) may differ from the cincinnal bracts in color and texture and is either straight or flexuose (zigzag). Rachis-internode length is measured between two adjacent cincinnal bracts (FIGURE 2, C). The cincinnal bracts are distichous or are spirally arranged due to twisting of the rachis. In some species (e.g., *H. xanthovillosa*) the rachis is only slightly twisted, making the cincinnal bracts subspirally arranged. Each bract is oriented at an angle of from 0 to 180° to the axis of the inflorescence (FIGURE 2, F). The cincinnal bract closest to the peduncle is the basal bract, is often sterile, and may be elongated and leaflike (FIGURE 2, D). The most conspicuous feature of a fertile plant is the colorful inflorescence. The cincinnal bracts are usually bright red and/or yellow but are sometimes green (e.g., *H. talamancana*) or even pink (e.g., *H. colgantea*). In some species (e.g., *H. stilesii, H. maculata*) the bracts are glabrous or essentially so, while in others (e.g., *H. magnifica, H. xanthovillosa*) the entire inflorescence may be covered by long, woolly hairs. Inflorescence and flower parts may be glabrous, puberulous, tomentose, velutinous, villous, or woolly. The term scurfy is used for any exfoliating vestiture that is easily removed by slight abrasion. The color and texture of the cincinnal bracts generally differ on the inside and outside surfaces. Because the cincinnal bracts decrease in size toward the apex of the inflorescence, those situated in the middle portion of the inflorescence (FIGURE 2, E) are best for comparative measurements. Bract length is measured from the rachis to the distal tip (FIGURE 3, Aa). The width is not measured across the open top since this changes with age, but from margin to margin as if the bract were spread out flat (FIGURE 3, Ab). Mean length/width quotients (l/w) are indicative of general bract shape. Bracts with quotients greater than 2 have long-acuminate apices; those with quotients less than 1.3 have short-acuminate or acute apices. The margins of the cincinnal bracts may be straight, revolute, or involute near the rachis.

FLORAL BRACTS

Each flower of the cincinnus is subtended by an individual floral bract (FIGURE 2, G). Often there are several basal floral bracts that do not directly subtend any individual flower. The floral bracts of some species are opaque and coriaceous, persisting through fruit development to protect maturing ovaries, while

FIGURE 2. Structure and measurements of inflorescences of *Heliconia*: A, peduncle; B, rachis; C, rachis internode length; D, basal cincinnal bract (sterile, with elongated leaflike extension); E, middle cincinnal bract; F, cincinnal bract angle with axis of inflorescence (e.g., 80°); G, floral bract.

those of other species are filmy or translucent and quickly decompose after anthesis. The floral bracts are variously colored and are textured abaxially; the adaxial surface is always glabrous.

FLOWERS

Although most floral characteristics are poorly preserved in pressed and dried plants, they can be quite helpful and even diagnostic when the flowers are fresh (or, in some cases, rehydrated). The flowers are hermaphroditic. Each cincinnus contains several to many (up to 50) flowers. The pedicel (FIGURE 3, Bg) is

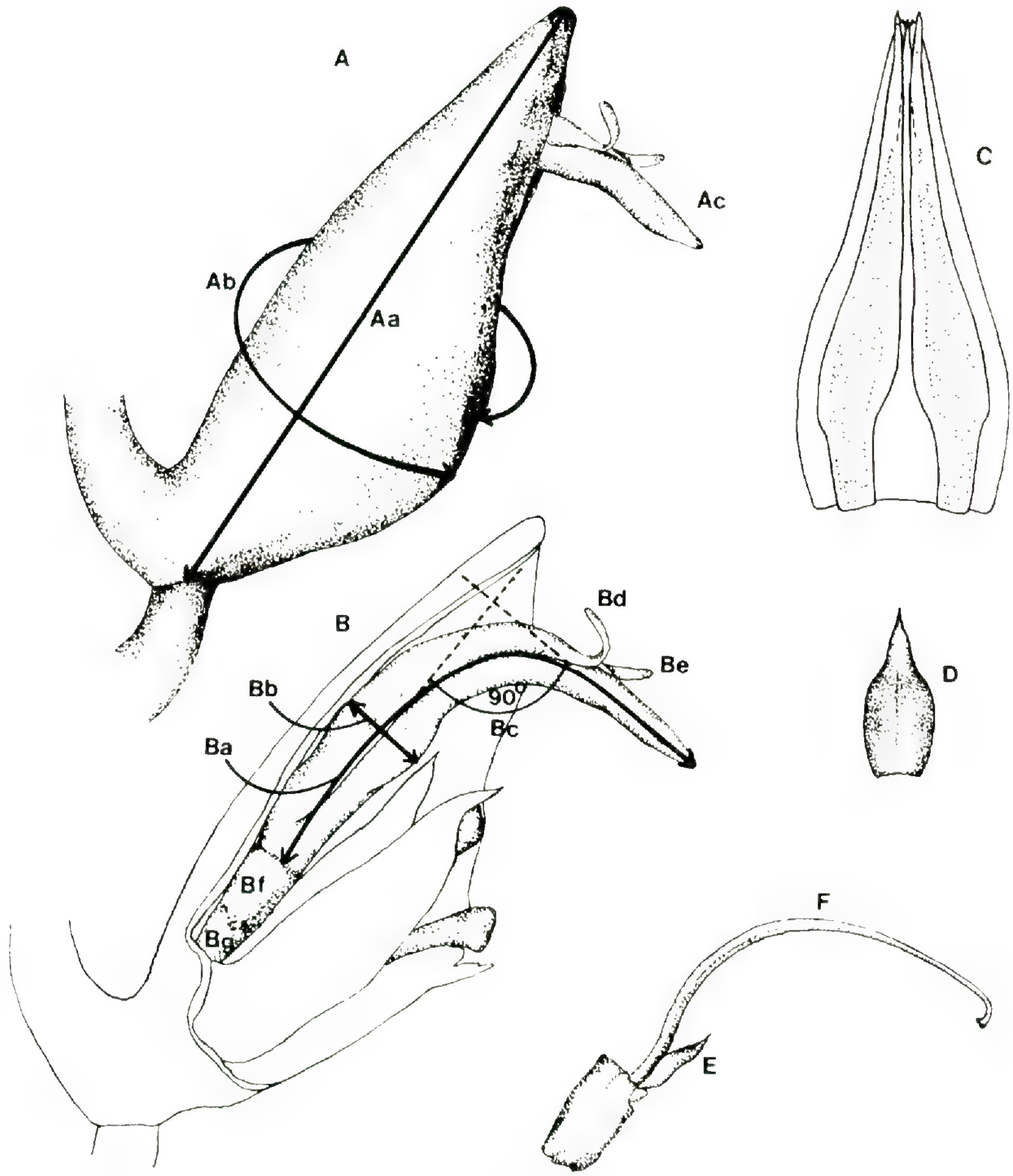


FIGURE 3. Structure and measurements of cincinnal bracts and flowers of *Heliconia*. A, cincinnal bract (Aa, length; Ab, width; Ac, flower protruding at anthesis). B, flower (Ba, perianth length; Bb, perianth width; Bc, perianth angle (e.g., 90°); Bd, apex of fused sepal reflexed; Be, apex of fused sepal not reflexed; Bf, ovary; Bg, pedicel). C, perianth, outer surface showing 2 sepals fused to partially spread-open corolla tube. D, E, staminodes: D, abaxial view; E, position relative to style, lateral view. F, style and stigma.

usually short and obscured by the floral bracts, but it can be exposed and distinctive in some species (e.g., *Heliconia collinsiana, H. trichocarpa*). The perianth is made up of two whorls united at the base that show varying degrees of fusion within and between whorls. At anthesis the single adaxial sepal becomes free from the other perianth members (FIGURE 3, Ac) and allows legitimate pollinators to enter the floral tube. The apices of the abaxial sepals are free from the corolla tube and may be reflexed (FIGURE 3, Bd) or not (FIGURE

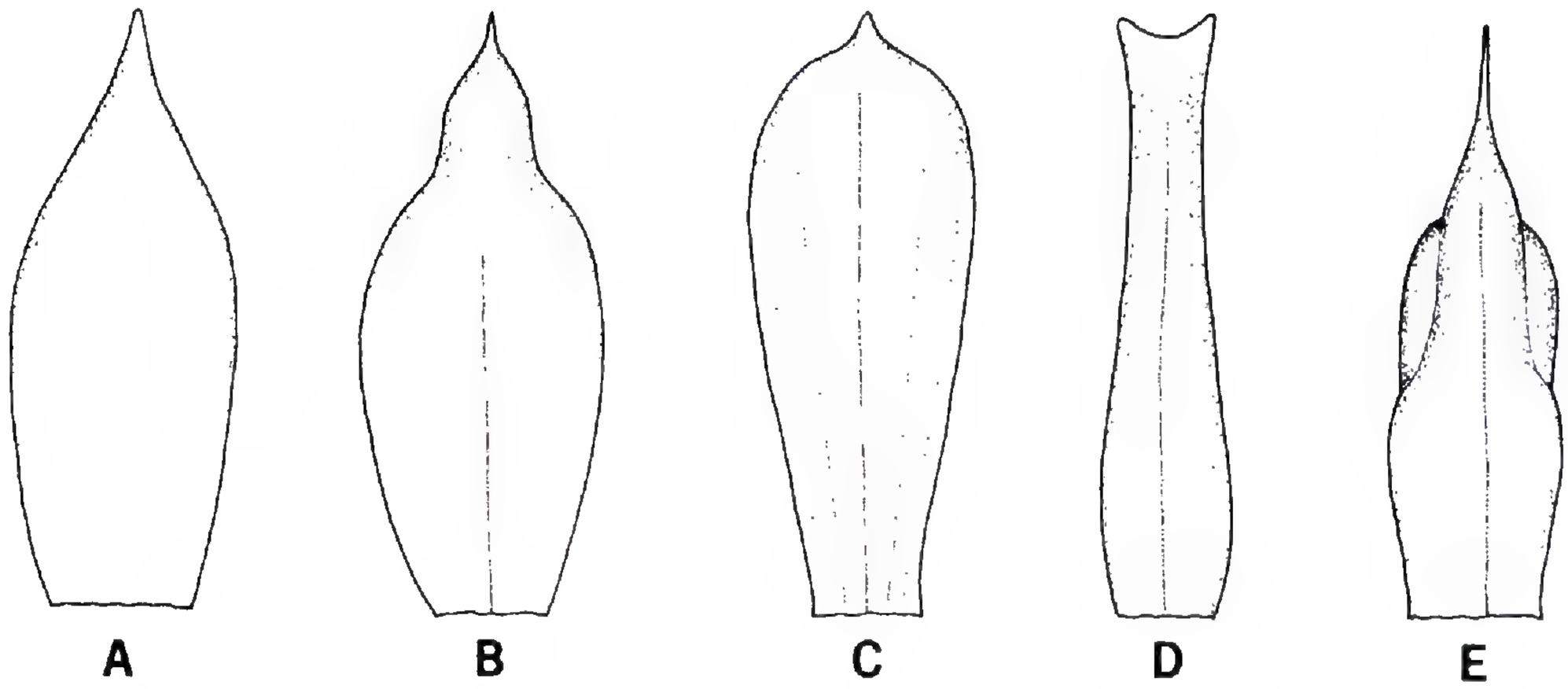


FIGURE 4. Staminode shape in *Heliconia* (not to scale): A, acuminate; B, cuspidate; C, apiculate; D, bidentate; E, lobed.

3, Be). The corolla tube is split along the margins of the two adaxial petals. The partially fused corolla tube is adnate to the two fused abaxial sepals (FIGURE 3, C) and lies opposite the free sepal. The free sepal opens above in erect inflorescences and below in pendent ones. In some species with erect inflorescences (e.g., *H. imbricata*), the pedicel is twisted, causing the flower to be resupinate and therefore to open in a fashion opposite to that described above. The perianth is usually yellow, varying from pale yellow to white at the base and to deep yellow apically. In some taxa the flowers are green (e.g., *H. secunda* var. *viridiflora*) or pinkish red (e.g., *H. mariae*). The sepals can be glabrous or pubescent, and the free sepal is sometimes velutinous or even woolly (e.g., *pogonantha* group). The length and curvature of the perianth tube reflects the length and curvature of the bill of the pollinating hummingbird. The length of the perianth is measured from its articulation with the ovary to the tip of the free adaxial sepal, following any curvature of the tube (FIGURE 3, Ba); the width at its widest diameter (FIGURE 3, Bb). Following the terminology of Andersson (1981), the perianth tube may be slightly curved (e.g., *H. collinsiana*), parabolic (e.g., *H. stilesii,* FIGURE 3, Bc), or sigmoid (e.g., *H. trichocarpa*).

Five stamens are fertile and produce viable pollen. The anthers, borne at the ends of long filaments that traverse the length of the perianth, are either connivent inside the corolla or flared outside of the perianth apex, and they dehisce longitudinally. The sixth stamen is replaced by a staminode located opposite the free sepal (FIGURE 3, D, E). This modified stamen does not produce pollen but may function in some species as a guide leading the hummingbird's tongue to the floral nectaries situated at the base of the style. The staminode ranges in length from 5 to 20 mm, and the apex may be acuminate, cuspidate, apiculate, dentate, or lobed (FIGURE 4).

The ovary (FIGURE 3, Bf) is inferior and three-locular. Each locule contains a single, basally attached ovule. The hypanthium is white, yellow, or green, and although it is usually glabrous, in some species (e.g., *Heliconia trichocarpa, H. maculata*) it is puberulous to pubescent. The style is much elongated, runs

the entire length of the perianth, and may be geniculate near the stigma (FIGURE 3, F). The lobed stigma is surrounded by the five fertile anthers at the apex of the perianth. Stigma morphology (degree of lobing and papilla development) appears to vary among species and may prove diagnostic in future studies.

FRUITS

Previous authors have described the fruits as berries, capsules, and "schizocarpic berries." An early study by Humphrey (1896) on seed development in the Zingiberales demonstrated that the mature fruit of *Heliconia* is a drupe with a stony endocarp enclosing each of the true seeds. This interpretation has recently been reconfirmed (B. Kirchoff, pers. comm.) and is accepted here. The outer pericarp is fleshy, and at maturity the surface layer becomes blue (Neotropical species) or red to orange (Paleotropical species). The fruits are very attractive to birds that disperse the seeds (Skutch, 1933; Stiles, 1979). Each drupe contains from one to three pyrenes. Each seed is surrounded by an exceptionally hard, roughened endocarpic envelope. Unlike the seeds of many other members of the order, those of *Heliconia* do not have an aril. The embryo is poorly differentiated at the time of seed maturity (Gatin, 1908), which may account for the delayed germination of *Heliconia* seeds often encountered by horticulturists.

A NOTE TO COLLECTORS

If an entire inflorescence cannot conveniently be collected, several representative sections (including cincinnal bracts from the base and apex) and the peduncle should be pressed. It is helpful if one cincinnal bract is cut open to reveal the flowers and floral bracts. A portion of the leaf showing the base of the blade and a portion showing the apex should also be collected and pressed.

Several vegetative and reproductive characters are of taxonomic importance but are usually not preserved after pressing and drying. Collectors should record the states of these characters from living specimens in the field:

Pseudostem: Color and vestiture
Leaf: Configuration
Musa-, *Canna*-, or *Zingiber*-like
Orientation
spiral or planar
Color of lamina (adaxial and abaxial)
Color of midrib (adaxial and abaxial)
Inflorescence: Position
terminal or arising from a basal shoot
Habit
erect or pendent
Color of peduncle
Color of rachis
Color of cincinnal bract (inside and outside)
Arrangement of cincinnal bracts
distichous or spirally arranged

Flower:
- Orientation
  - resupinate or not resupinate
- Color of perianth and ovary
- Curvature of apices of fused sepals
  - reflexed or straight
- Orientation of anthers
  - flared outside perianth apex or connivent inside apex
- Shape of staminode

POLLEN

The pollen of *Heliconia* and most of its allies in the Zingiberales (excluding Zingiberaceae and Costaceae) is characterized by a sporoderm significantly different in structure from that of most angiosperms. The normally elaborate protective exine is reduced to a few spinules and a thin (0.08 μm) connective layer covering the surface. The intine, contrastingly, is much thickened (8 μm) and structurally complex (Erdtman, 1966; Kress *et al.,* 1978). Radially striate channels perforate the intine of the distal hemisphere, while a more homogeneous but stratified intine characterizes the proximal hemisphere.

Recently, the ultrastructure (Kress *et al.,* 1978), cytochemistry (Kress & Stone, 1982), and ontogeny (Stone *et al.,* 1979) of *Heliconia* pollen have been described in detail. A systematic comparison of pollen of 27 Central American species of *Heliconia* has been published elsewhere (Kress & Stone, 1983). The results of that study that are pertinent to the present taxonomic revision are briefly summarized here.

The pollen of heliconias with pendent inflorescences is 46–65 μm in polar diameter and 54–86 μm in equatorial diameter. The distal radius is 24–56 μm; the proximal radius 8–29 μm. The grains may be euoblate, suboblate, or oblate-spheroidal, and isopolar, subisopolar, or heteropolar. In addition to variation in size, the shape and sculpturing of each hemisphere, which are generally different in a single grain, also vary among species. The distal hemisphere is usually convex (but may be subconvex or planar) and sometimes is truncate or shows constrictions parallel to the equatorial plane. The proximal hemisphere may be convex, subconvex, planar, or subconcave. Although the entire wall of the distal hemisphere resembles the germination aperture of more conventional angiosperm pollen, the grains appear inaperturate. However, the pollen tube invariably emerges from a central region at the distal pole. This central region is the functional germination "aperture" and is often structurally distinct. It may protrude from the pole and be elongated, or it may be rather flattened and partially sunken into the distal surface. Sculpturing of the reduced exine ranges from psilate to granulose to verrucose to spinulose or minutely spinulose. In most species the pattern is different on the two hemispheres.

Statistical analysis of both quantitative and qualitative pollen characters support the recognition of four groups among the 19 species with pendent inflorescences studied: the *pogonantha* group, including *Heliconia pogonantha, H. magnifica, H. ramonensis, H. danielsiana, H. xanthovillosa,* and *H. mariae*; the *curtispatha* group, comprising *H. curtispatha* and *H. stilesii*; the *trichocarpa*

group, with *H. trichocarpa, H. colgantea, H. necrobracteata, H. maculata,* and *H. talamancana*; and the *nutans* group, containing *H. nutans, H. collinsiana, H. secunda, H. platystachys,* and *H. marginata.* The polar diameter, the degree of grain polarity, the shape of each hemisphere, the shape of the germination aperture, and the sculpturing of the proximal hemisphere are of particular taxonomic value in delimiting these groups, which are also characterized by other morphological traits (see section on phylogeny). The pollen of *H. sessilis,* however, shares some character states with each of the four groups and so is not easily placed in any of them.

Pollen of the *pogonantha* type (FIGURE 5, A) is large (60–65 × 81–86 μm), euoblate to oblate-spheroidal, and heteropolar, with a convex-truncate, spinulose distal hemisphere and a planar, psilate proximal hemisphere. The germination aperture is distinct, flattened, and somewhat sunken.

Pollen of the *curtispatha* type (FIGURE 5, B) is medium sized (53–57 × 66–70 μm), suboblate, and isopolar, with a convex to subconvex, spinulose distal hemisphere and a convex, minutely spinulose proximal hemisphere. The germination aperture is distinct and usually sunken.

Pollen of the *trichocarpa* type (FIGURE 5, C) is medium sized (49–55 × 67–79 μm), euoblate, and isopolar, with a subconvex to planar, verrucose to spinulose distal hemisphere and a convex, granulose to minutely spinulose proximal hemisphere. The germination aperture is indistinct except for an occasional slight depression in the center of the planar distal face.

Pollen of the *nutans* type (FIGURE 5, D) is relatively small (43–56 × 54–76 μm), euoblate to oblate-spheroidal, and subisopolar, with a convex, often constricted, spinulose distal hemisphere and a subconvex to planar, psilate to verrucose proximal hemisphere. The germination aperture is distinctly protruding and sometimes quite elongate.

CYTOLOGY

The cytology of *Heliconia* is poorly known. Of the 14 species for which chromosome numbers have been reported (Bisson *et al.,* 1968; Mahanty, 1970), fewer than half have legitimate names and several are not identified to species. In none of the studies was any voucher specimen designated, and it is unlikely that the majority of specimens were identified correctly. In addition, since only one of the species listed (*H. nutans,* if identified correctly) has a pendent inflorescence, the chromosome counts reported are of little help in the present study.

HABITAT AND GEOGRAPHIC DISTRIBUTION

Members of the genus *Heliconia* are distributed primarily throughout the New World tropics from the Tropic of Cancer in Central Mexico to the Tropic of Capricorn in South America. Most species inhabit moist or wet regions, but some are found in seasonally dry areas. Although heliconias attain their most luxuriant vegetative growth in the humid lowland tropics at elevations below 500 meters, the greatest numbers of species (many locally endemic) are found

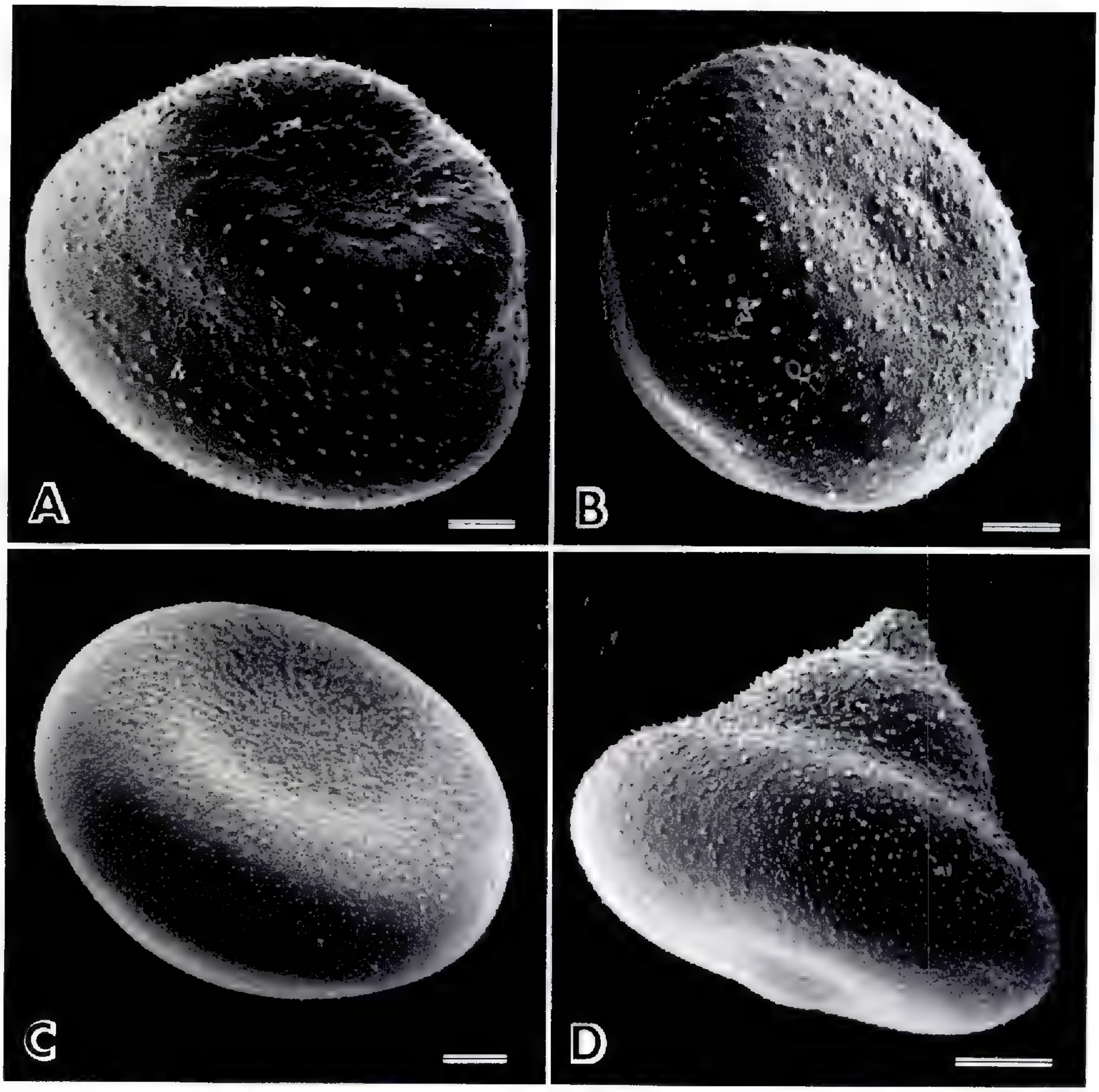


FIGURE 5. Pollen types of *Heliconia* with pendent inflorescences: A, *pogonantha* type (*H. pogonantha,* distal view); B, *curtispatha* type (*H. stilesii,* distal view); C, *trichocarpa* type (*H. trichocarpa,* distal view); D, *nutans* type (*H. nutans,* equatorial view). Scale = 10 μm.

in middle-elevation rain and cloud-forest habitats. Few species occur above 2000 meters.

The most conspicuous members of the genus inhabit open sites in secondary growth along roadsides, on river banks, and in forest light gaps. With increased destruction by man of the tropical rain forest, these species readily invade and colonize the newly opened areas. Other species never attain such extensive vegetative growth and are restricted to the more shaded habitats of the primary forest. These latter species are often locally endemic and are fast becoming extinct as destruction of the forest accelerates.

Species of *Heliconia* with pendent inflorescences are found in Mexico, Central America, South America, and Melanesia (the Solomon Islands). None is known from the West Indies. The taxa treated in this revision are distributed from

Michoacán in southern Mexico to Darién in Panama. Most species occurring north of Costa Rica are found on the wet Atlantic slopes and coastal plains. In Costa Rica and some parts of Panama, the Pacific slopes have sufficient rainfall to support a number of species of *Heliconia.* In these countries several pairs of closely related species (e.g., *H. curtispatha/H. stilesii, H. trichocarpa/ H. colgantea, H. pogonantha/H. danielsiana*) are allopatrically distributed on opposite sides of the central cordillera. No differences in habitat or geographic distribution are apparent between species with pendent and erect inflorescences, and species of the two inflorescence habits are often sympatric.

A curious disjunct group of heliconias is found in the Old World tropics. These heliconias are distributed from Samoa westward to the central Indonesian island of Sulawesi. These plants undoubtedly belong in the genus, even though a separate generic name, *Heliconiopsis,* has been suggested (Miquel, 1859). Green (1969) included all of the Old World taxa in a single species, *Heliconia indica* Lam. A taxonomic treatment currently in preparation (Kress, unpubl.) recognizes eight species occurring in this area, some locally endemic to specific islands or land masses. Two of these species (both unpublished) have pendent inflorescences.

POLLINATION AND REPRODUCTIVE BIOLOGY

Several original reports and review papers describing the reproductive biology of *Heliconia* have recently appeared (Stiles, 1975, 1979; Kress, 1981b, 1983a, 1983b, in press). Only the taxonomically important aspects will be summarized here; see the cited papers for details.

In the Neotropics hummingbirds are the exclusive pollinators of *Heliconia.* Species-specific relationships between birds and plants are rare. Any *Heliconia,* however, can be categorized as being visited primarily either by traplining hermit hummingbirds or by territorial nonhermit hummingbirds (Linhart, 1973; Stiles, 1975). Physiological self-incompatibility is uncommon in the genus; most species that have been tested so far are self-compatible (Kress, 1983a). Plant/bird morphological specialization, hummingbird foraging behavior and habitat, and phenological differences may all serve as isolating mechanisms that prevent pollen exchange between species (Stiles, 1975, 1978; Kress, 1983b, in press). Of all the mechanisms restricting interspecific gene flow in *Heliconia,* physiological regulation of foreign pollen germination and pollen-tube growth at the stigmatic surface and in the style is the most important (Kress, 1983b). I have found that in the species tested, pollen of any one species was inhibited at the stigma, within the stylar tissue, or within the ovary of most other species, and that the site of inhibition depended on the species combination and the direction of the cross. Cross-compatibility was uncommon, and hybrid seed was obtained from very few hybrid combinations. Natural hybridization is also rare (Kress, 1981b, 1983b, in press), especially considering the large number of sympatric taxa in the genus. The few hybrids between species with pendent inflorescences known from the wild are discussed in the section on natural hybridization.

The specificity of the interspecific crossability barriers is significant from a

taxonomic standpoint. In my study (Kress, 1983b) at Las Cruces Tropical Botanical Garden in Costa Rica, nine species with pendent inflorescences were crossed in nearly all reciprocal combinations. Each species was categorized by the ability of the style to accept foreign pollen tubes and the ability of the pollen to grow in foreign styles. Species were then grouped together according to the main type of crossability barrier that characterized the pistil and pollen of each (see TABLE 3). For example, in *Heliconia pogonantha, H. danielsiana,* and *H. colgantea* foreign pollen is inhibited at the stigmatic surface, and pollen of these species is inhibited on the stigma of most foreign species. In contrast, although foreign pollen is nearly always inhibited at the stigma in *H. collinsiana* and *H. nutans,* the pollen of these species breaks the stigmatic barrier of most other species, and pollen-tube growth is arrested in the style. In the case of *H. mariae, H. stilesii,* and *H. curtispatha,* foreign pollen is stopped at the stigma and/or style, and their own pollen does not penetrate foreign stigmas. *Heliconia trichocarpa* has the least specific pistil- and pollen-inhibition barriers of the nine species tested. When compared to the groups of species recognized by their vegetative, floral, and pollen characters (see section on phylogeny), the groups defined by crossability barriers are nearly the same, even though the placement of some species (e.g., *H. colgantea* and *H. mariae*) is inconsistent. Presence of specific crossability barriers appears to reflect the phylogenetic history of at least some species of *Heliconia.*

PHYLOGENY

One goal of taxonomic investigations is to reconstruct phylogenetic relationships. Phylogenetic systematics (*sensu* Hennig, 1966), or cladistics, provides a logical and repeatable method for formulating hypotheses of phylogeny and for devising biological classifications (Bremer & Wanntorp, 1978; Eldredge & Cracraft, 1980; Wiley, 1981). Cladistics requires that a classification recognize only monophyletic groups (groups that include all and only the descendents of a common ancestor) and hence be isomorphic with the hypothetical genealogy of the taxa. Monophyletic groups can only be recognized on the basis of shared uniquely derived character states (synapomorphies); shared primitive or ancestral character states (symplesiomorphies) can only define paraphyletic groups (those that include some but not all of the descendents of an ancestor). The most compelling argument for adoption of phylogenetic systematics and for using cladistic hypotheses as the basis for classification is that a common genealogy is the sole factor that unites all organisms.

A cladistic analysis of the 19 Central American species of *Heliconia* with pendent inflorescences (hereafter referred to as "pendent species") was undertaken in an attempt to answer two questions: 1) What are the genealogical relationships of the taxa? 2) Is the group of species with pendent inflorescences monophyletic (i.e., is the pendent inflorescence habit shared by these species a synapomorphy that defines a monophyletic group)? The first question can be answered by constructing a cladogram for the taxa, as outlined below. A definitive answer to the second question is more difficult to obtain using only the 19 species included in the revision because these species represent a subset

TABLE 3. **Main sites of pistil and pollen inhibition in species of Heliconia crossed at Las Cruces Tropical Botanical Garden.***

SPECIES	MAIN SITE OF INHIBITION	
	Pistil	**Pollen**
H. colgantea *H. danielsiana* *H. pogonantha*	Stigma	Stigma
H. collinsiana *H. nutans*	Stigma	Stigma/style
H. curtispatha *H. mariae* *H. stilesii*	Stigma/style	Stigma
H. trichocarpa	Stigma/style	Stigma/style

*Table from Kress, 1983b, © Annals of Botany Company, 1983; reprinted with permission.

of all heliconias. To provide at least a tentative answer to this question, five species with erect inflorescences (hereafter referred to as "erect species") were added to the phylogenetic analysis of the pendent species. If either inflorescence habit is uniquely derived in *Heliconia,* then it should define a monophyletic group of species, all of which have that inflorescence type.

METHODS, TAXA, AND CHARACTERS

The basic methodology of phylogenetic systematics includes definition and delimitation of monophyletic taxa as operational units for the analysis; careful and accurate assignment of character states to taxa based upon sound hypotheses of homology; formulation of hypotheses of character-state polarity using outgroup comparison; construction of a cladogram of the taxa; careful mapping of character-state changes on the cladogram and reassessment of the original hypotheses of monophyly, homology, and polarity; and, if appropriate, devising a hierarchical classification based on the monophyletic groups defined by the cladogram.

The results of phylogenetic systematic studies are only meaningful if the taxa under investigation are monophyletic (Hennig, 1966; Eldredge & Cracraft, 1980; Arnold, 1981; Wiley, 1981). It is normally assumed that species are monophyletic. In the present analysis each of the species used as a unit taxon for construction of the cladograms has a suite of apomorphies that suggests it is a monophyletic lineage (see individual species descriptions). The monophyly of the entire group is a central question of the investigation. The presence of a pendent inflorescence in all of the species suggests that the 19 Central American species as a group may be a monophyletic lineage. If the pendent inflorescence is a uniquely derived character in *Heliconia,* the exclusion of all South American pendent species automatically makes it likely that the group is paraphyletic. Nonetheless, the limitations that result from not including all members of a monophyletic group in a phylogenetic analysis do not invalidate the

cladogram as the best hypothesis of relationships of the included taxa. The first cladogram presented here, which includes only the Central American species with pendent inflorescences, therefore provides a testable hypothesis of the genealogical relationships of these taxa.

To test the hypothesis of monophyly of the pendent species, a second cladogram incorporating five additional species with erect inflorescences was constructed. These particular five species were chosen for several reasons. Comparative data on character-state distribution (especially information on pollen characters) were available for the species. The five species are representatives of both of Griggs's (1915) subgenera (*Taeniostrobus* and *Stenochlamys*) and three of his five unranked supraspecific groups that contain erect species (*Imbricatae, Distantes,* and *Cannoideae*). The majority of the pendent species fall into his sixth supraspecific taxon, *Pendulae. Heliconia imbricata* and *H. wagneriana,* together with *H. mariae* and *H. curtispatha* (with pendent inflorescences), were classified in Griggs's *Imbricatae,* a group of species with imbricate or overlapping cincinnal bracts. *Heliconia wagneriana* has most recently been included by Andersson (1981) in sect. HELICONIA, which contains members of Griggs's *Imbricatae* and *Champneianae. Heliconia latispatha* and *H. tortuosa* were members of Griggs's *Distantes,* a group of species with erect inflorescences and a *Musa*-like shoot habit. The latter species is very similar to *H. secunda* (with a pendent inflorescence) and therefore suggests some affinity between pendent and erect species (Stiles, 1979). *Heliconia mathiasiae,* although not yet described when Griggs developed his classification, would have been included in his *Cannoideae* because of its "cannoid" (here called *Zingiber*-like) shoot habit. The morphological diversity of the five erect species and their representation of most of Griggs's supraspecific groups of *Heliconia* insures that a reasonable sample of different species was chosen to test the hypothesis of the monophyletic status of the pendent species.

If synapomorphies could easily be recognized and distinguished from similarity due to homoplasy or plesiomorphy, delimitation of monophyletic groups would be simple and unambiguous. The fact that accurate identification of synapomorphies is difficult requires careful and explicit character analysis, especially with regard to comparison of homologous structures. The only phylogenetically useful concept of homology is genealogical: two taxa share a feature because it was present in their common ancestor (Eldredge & Cracraft, 1980). The hypotheses of homology required to construct a cladogram, however, must initially be based on indirect sources of evidence (e.g., similarity in position, anatomy, or development). The resulting cladogram, representing the largest nested set of mutually consistent, hierarchically correlated characters, will then provide a test of these hypotheses of homology. Characters not consistent with the cladogram (those requiring multiple independent origins or reversals) are homoplasious and suggest that the initial hypotheses of homology for these characters were incorrect and in need of reevaluation.

Character states assigned to each of the species (see TABLE 4) for the 30 characters used in the analysis were determined for at least three individuals per population for one to several populations throughout the geographic range of each taxon (TABLE 5). Discrete, nonoverlapping states for characters with

potentially continuous distributions (e.g., overall height, inflorescence size) were determined by the use of bar graphs. Whenever possible, intraspecifically variable characters were eliminated from the analysis. In some cases in which a species was variable for a given character, the state present in its closest relatives was chosen as the primitive state for the variable species. These characters were then reevaluated after the cladogram was constructed. For example, the four varieties of *Heliconia pogonantha* vary in the presence of hairs on the inflorescence. The velutinous perianth present in all varieties of this species is also found in other closely related heliconias that have velutinous to woolly inflorescences. A hairy inflorescence was therefore chosen as the primitive state in the variable *H. pogonantha.*

Outgroup comparison, the most logically justifiable method for determining character-state directionality (Lundberg, 1972; Eldredge & Cracraft, 1980; Stevens, 1980; Watrous & Wheeler, 1981), was used to polarize the characters in *Heliconia* (see TABLE 6). By general consensus (TABLE 2; Baker, 1893; Lane, 1955; Tomlinson, 1962; Dahlgren & Clifford, 1982), members of the "banana-like" families of the Zingiberales, especially the Musaceae and Strelitziaceae, are considered to be the closest relatives of *Heliconia.* Several shared features of floral morphology unite the Heliconiaceae most closely with the Musaceae, and a recent attempt to construct a phylogeny of the entire order (Dahlgren & Rasmussen, 1983) recognizes these two families as sister groups. For the cladistic analyses of *Heliconia,* the two genera of the Musaceae *sensu stricto, Musa* and *Ensete,* were chosen as the outgroup. Information on character states in the Musaceae was taken from Lane (1955), Tomlinson (1962), Erdtman (1966), Argent (1976), Dahlgren and Clifford (1982), and Kress and Stone (unpubl.). Character states universally present in this family were scored as primitive in *Heliconia.* Characters not present in the outgroup (e.g., hummingbird pollination), or present with more than one state (e.g., inflorescence habit), were not used. Multistate characters were coded as either unidirectional ($0 \rightarrow 1 \rightarrow 2$; characters 8, 12, 17–21, 24, 25) or bidirectional ($0 \leftarrow 1 \rightarrow 2$; characters 7, 10, 11, 13) according to indirect evidence for character-state homologies (see TABLE 6). For clarity, autapomorphies for single species of *Heliconia* and character states present in the genus but not in the species with pendent inflorescences were also eliminated. In total, the 30 characters used in the analysis contained 44 character-state changes or evolutionary steps (TABLE 6).

The cladogram was constructed using Farris's Wagner '78 computer program. The program is based on a Wagner tree algorithm (Kluge & Farris, 1969; Farris, 1970) that produces the most parsimonious tree without placing any restrictions on homoplasious evolution. One problem with the program is that it may produce cladograms of different lengths depending on the order in which the taxa appear in the data file (Coombs *et al.,* 1981). However, in these analyses the same cladograms were produced regardless of the order in which the taxa were submitted.

RESULTS

CLADOGRAMS. The cladogram of the 19 species with pendent inflorescences (cladogram I; FIGURE 6), including a hypothetical ancestor having all hypoth-

TABLE 4. **Taxon by character matrix for 24 species of Heliconia and 30 characters.**

	Character*																													
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
ANC†	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CLG††	1	0	0	1	1	1	0	2	0	0	1	3	0	1	1	1	1	1	2	0	2	0	0	1	0	1	0	0	0	0
COL	0	1	0	0	0	1	0	1	0	1	1	1	1	1	1	0	1	2	1	1	0	0	0	2	1	1	1	1	0	0
CUR	0	0	0	0	0	0	0	0	1	0	0	2	1	0	0	0	1	1	1	0	1	0	0	2	0	1	1	0	1	0
DAN	0	0	1	0	0	0	2	0	1	2	2	3	2	0	0	0	0	0	2	2	0	1	0	2	2	0	1	0	1	1
IMB	0	0	0	0	0	1	1	0	1	1	1	3	1	1	0	0	1	1	1	1	0	0	1	2	1	0	1	1	0	0
LAT	1	0	0	0	0	1	1	1	0	1	1	1	1	0	0	0	2	2	2	1	0	0	1	2	2	1	1	1	0	0
MAC	1	0	0	1	1	1	1	2	0	1	1	3	1	1	0	1	1	1	2	0	1	0	0	1	0	1	0	0	0	0
MAG	0	0	1	0	0	0	2	0	1	2	2	3	2	0	0	0	0	0	1	2	0	1	0	2	2	0	1	0	1	1
MAR	0	0	0	0	0	0	1	0	0	1	1	2	0	0	0	0	1	1	2	2	1	1	0	2	2	0	1	0	1	1
MAT	0	0	0	0	1	1	1	2	0	1	1	1	1	1	0	0	1	1	2	0	2	0	0	1	0	1	0	0	0	0
MRG	1	0	0	0	0	1	0	1	1	0	1	1	1	1	0	0	1	1	2	1	0	0	0	2	1	1	1	1	0	0
NEC	0	0	0	1	1	1	0	1	0	1	1	3	1	1	1	0	1	1	2	0	2	0	0	1	0	1	0	0	0	0
NUT	1	0	0	0	0	1	0	1	0	1	1	1	1	1	0	0	2	2	1	1	0	0	1	2	1	1	1	1	0	0
PLT	1	1	0	0	0	1	0	1	0	0	0	1	1	1	0	1	0	2	1	1	0	0	1	2	1	1	1	1	0	0
POG	0	0	0	0	0	0	2	0	1	2	2	3	2	0	0	0	0	0	2	2	0	1	0	2	2	0	1	0	1	1
RAM	0	0	1	0	0	0	2	0	1	2	2	3	2	0	0	0	0	0	2	2	0	1	0	2	2	0	1	0	1	1
SEC	1	0	0	0	0	1	1	1	0	1	1	1	1	1	0	0	2	2	2	1	0	0	1	2	1	1	1	1	0	0
SES	0	0	0	0	0	0	0	0	1	1	1	3	1	0	0	0	1	1	2	1	1	0	0	2	2	0	1	0	1	1
STI	0	0	0	0	0	0	1	0	1	0	0	2	1	0	0	0	1	1	1	0	1	0	0	2	0	1	1	0	1	0
TAL	0	0	0	1	1	1	1	2	0	1	1	3	0	1	1	1	1	1	2	0	1	0	0	1	0	1	0	0	0	0
TOR	1	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	2	2	1	1	0	0	1	2	1	1	1	1	0	0
TRI	1	0	0	1	1	1	0	2	0	0	1	3	1	1	1	1	1	1	2	0	2	0	0	1	0	1	0	0	0	0
WAG	1	0	0	0	0	1	1	0	0	1	1	1	1	0	0	0	0	0	1	1	0	0	0	2	1	0	1	1	0	0
XAN	0	0	1	0	0	0	2	0	1	2	2	3	2	0	0	0	0	0	1	2	0	1	0	2	2	0	1	0	1	1

*See Table 6 for character states and polarity.

†Hypothetical ancestor having all primitive character states.

††For species abbreviations see Table 5.

TABLE 5. **Field collections of Heliconia species from which character-state data were taken for phylogenetic analyses and descriptions of taxa.**

TAXON*	COLLECTION DATA†
H. colgantea Daniels & Stiles (CLG)	Costa Rica: Puntarenas, *77-878*
H. collinsiana Griggs (COL) var. *collinsiana*	Guatemala: Alta Verapaz, *77-747* Esquintla, *77-753* Nicaragua: Managua, *77-758*
var. *velutina* Kress	Guatemala: Quezaltenango, *77-756*
H. curtispatha Petersen (CUR)	Costa Rica: Limón, *77-789* Nicaragua: Zelaya, *77-759* Panama: Panamá, *77-864*
H. danielsiana Kress (DAN)	Costa Rica: Puntarenas, *77-821* San José, *79-1097*
******H. imbricata* (Kuntze) Baker (IMB)	Costa Rica: Heredia, *79-1101*
******H. latispatha* Bentham (LAT)	Costa Rica: Heredia, *79-1100*
H. maculata Kress (MAC)	Panama: Colón, *80-1240*
H. magnifica Kress (MAG)	Panama: Panamá, *77-850, 80-1246*
H. marginata (Griggs) Pittier (MRG)	Costa Rica: Puntarenas, *77-804, 79-1095*
H. mariae J. D. Hooker (MAR)	Guatemala: Petén, *77-743* Alta Verapaz, *77-745* Costa Rica: Alajuela, *77-771* Heredia, *79-1104* Limón, *77-794* Nicaragua: Zelaya, *77-761* Panama: Canal Zone, *77-855*
******H. mathiasiae* Daniels & Stiles (MAT)	Costa Rica: Heredia, *79-1105*
H. necrobracteata Kress (NEC)	Panama: Coclé, *77-842, 80-1158*
H. nutans Woodson (NUT)	Panama: Chiriquí, *77-822, 79-1088, 79-1089a, 79-1089b, 82-1344, 82-1345, 82-1355, 82-1368* Veraguas, *82-1410*
H. platystachys Baker (PLT)	Costa Rica: Puntarenas, *77-803* Panama: Canal Zone, *77-860*
H. pogonantha Cuf. (POG) var. *pogonantha*	Costa Rica: Heredia, *77-778, 79-1102* Nicaragua: Zelaya, *77-760*
var. *holerythra* Daniels & Stiles	Costa Rica: Limón, *77-790* Panama: Colón, *77-874*
var. *pubescens* Daniels & Stiles	Costa Rica: Cartago/Limón, *77-788*
var. *veraguasensis* Kress	Panama: Veraguas, *77-825*
H. ramonensis Daniels & Stiles (RAM) var. *ramonensis*	Costa Rica: Alajuela, *77-764*
var. *glabra* Kress	Panama: Coclé, *83-1589*
var. *lanuginosa* Kress	Panama: Chiriquí, *83-1600, 83-1602*
var. *xanthotricha* Kress	Panama: Coclé, *77-840, 80-1161*

TABLE 5 (*continued*).

TAXON*	COLLECTION DATA†
H. secunda R. R. Smith (SEC) var. *secunda*	Costa Rica: Heredia, *77-773, 77-776*
var. *viridiflora* Daniels & Stiles	Costa Rica: Guanacaste, *80-1216*
H. sessilis Kress (SES)	Panama: Colón, *77-871, 80-1241*
H. stilesii Kress (STI)	Costa Rica: Puntarenas, *79-1096* San José, *77-799*
H. talamancana Daniels & Stiles (TAL)	Costa Rica: Limón, *77-791*
***H. tortuosa* Griggs (TOR)	Costa Rica: Puntarenas, *78-944*
H. trichocarpa Daniels & Stiles (TRI)	Costa Rica: Alajuela, *77-767, 77-804* Cartago, *77-787* Heredia, *79-1109* Panama: Veraguas, *77-832*
***H. wagneriana* Petersen (WAG)	Panama: Colón, *80-1244*
H. xanthovillosa Kress (XAN)	Panama: Panamá, *80-1233, 83-1565*

*Abbreviations for species names used in phylogenetic analysis are given in parentheses following the author. Species with erect inflorescences are indicated by a double asterisk (**).

†All collections were made by the author and are deposited in the Duke University Herbarium (DUKE). For complete locality information, see "Specimens Examined" under the appropriate species description.

esized plesiomorphic character states, had a total length of 84 evolutionary steps. Forty steps were homoplasious. The index of consistency (Kluge & Farris, 1969), which is the total length of the cladogram minus the homoplasies divided by the total length, was .524. This index permits comparisons of the degree of homoplasy or parsimony between cladograms constructed from different character sets or containing different taxa. Character-state changes for each of the 30 characters are indicated on the cladogram.

The second cladogram (cladogram II; FIGURE 7), which includes the 19 pendent and the five erect species, had a total length of 96 steps. Fifty-two steps were homoplasious, and the index of consistency was .458. The same basic topology of the four monophyletic groups of pendent species present in cladogram I was maintained in cladogram II. The five erect species do not form a monophyletic lineage. Three of the erect species are intercalated within pendent lineages: *Heliconia mathiasiae* in the *trichocarpa* group, and *H. latispatha* and *H. tortuosa* in the *nutans* group. The remaining two erect species, *H. wagneriana* and *H. imbricata,* constitute two single-species monophyletic groups that do not share a most recent common ancestor.

CHARACTER ANALYSIS. Twenty of the 30 characters used in the construction of cladogram I had at least one uniquely derived state (characters 2–5, 7–13, 20, 22–25, 27–30). Some characters, such as overall height (character 1) and pollen-grain shape (characters 19, 21), were homoplasious and not phylogenetically

TABLE 6. **Thirty characters used in the phylogenetic analyses.**

CHARACTER	CHARACTER STATES (values)
1. Overall shoot height	>4 m (0)* <4 m (1)
2. Pseudostem surface	not glaucous (0)* glaucous (1)
3. Pseudostem vestiture	absent (0)* present (1)
4. Leaf-blade shape	oblong-elliptic (0)* oblanceolate (1)
5. Shoot aspect	erect (0)* horizontal/oblique (1)
6. Inflorescence size (number of bracts)	large (>20) (0)* small (<20) (1)†
7. Rachis vestiture	essentially absent (1)* short hairs (0)† long hairs (2)
8. Cincinnal-bract length/width quotient	<1.4 (0)* 1.5–2.0 (1)† >2.0 (2)
9. Cincinnal-bract margins	straight (0)* involute at base (1)
10. Cincinnal-bract outer vestiture	essentially absent (1)* short hairs (0) long hairs (2)
11. Cincinnal-bract inner vestiture	essentially absent (1)* short hairs (0) long hairs (2)
12. Flower shape	straight (0)* slightly curved (1) parabolic (2)† sigmoid (3)
13. Vestiture at perianth apex	essentially absent (1)* short hairs (0) long hairs (2)
14. Anther orientation	connivent inside perianth apex (0)* flared outside perianth apex (1)†
15. Staminode length	<1 cm (0)* >1 cm (1)
16. Ovary vestiture	absent (0)* short hairs (1)
17. Pollen polar diameter	≥60 μm (0)* 49–59 μm (1)† ≤48 μm (2)
18. Pollen equatorial diameter	≥80 μm (0)* 65–79 μm (1)† ≤64 μm (2)
19. Overall pollen shape (P/E)	oblate-spheroidal (≥.88) (0)* suboblate (.76–87) (1) euoblate (≤.75) (2)†

TABLE 6 (*continued*).

CHARACTER	CHARACTER STATES (values)
20. Pollen polarity (DR/PR)	isopolar (<2) (0)* subisopolar (2–5) (1) heteropolar (>5) (2)
21. Pollen distal-hemisphere shape I	convex (0)* subconvex (1)† planar (2)
22. Pollen distal-hemisphere shape II	not truncate (0)* truncate (1)
23. Pollen distal-hemisphere shape III	not constricted (0)* constricted (1)
24. Pollen distal-hemisphere sculpturing	psilate (0)* granulose–minutely spinulose (1)† spinulose (2)
25. Pollen proximal-hemisphere shape	convex (0)* subconvex (1) planar (2)
26. Pollen proximal-hemisphere sculpturing	psilate (0)* granulose–minutely spinulose (1)†
27. Pollen germination aperture I	indistinct (0)* distinct (1)
28. Pollen germination aperture II	not protruding (0)* protruding (1)
29. Pollen germination aperture III	not sunken (0)* sunken (1)
30. Pollen germination aperture IV	not flattened (0)* flattened (1)

*Character state present in outgroup and originally coded as primitive for *Heliconia*.
†Character state present in most recent common ancestor of species in cladogram I.

informative. Several other features of the pollen grains (characters 22–25, 27–30) proved quite useful in delimiting monophyletic lineages (also see Kress & Stone, 1983). Long hairs on inflorescences and flowers (characters 7, 10, 11, 13) are uniquely derived in one monophyletic group (see below), whereas short hairs appear to have evolved independently in several lineages and are therefore not homologous in all heliconias in which they occur.

The large number of character-state changes (characters 6–8, 12, 14, 17–19, 21, 24, 26) occurring between the hypothetical ancestor and the extant heliconias in cladogram I suggests that the most recent common ancestor of these pendent heliconias did not have some of the originally assigned plesiomorphic states present in the outgroup. These eleven characters were recoded so that the primitive state is the one present not in the outgroup but in the most recent common ancestor (see TABLE 6). In addition, states of multistate characters present in the outgroup but not in the pendent heliconias were eliminated from the transformation series of characters 12, 21, and 24. The result is a more

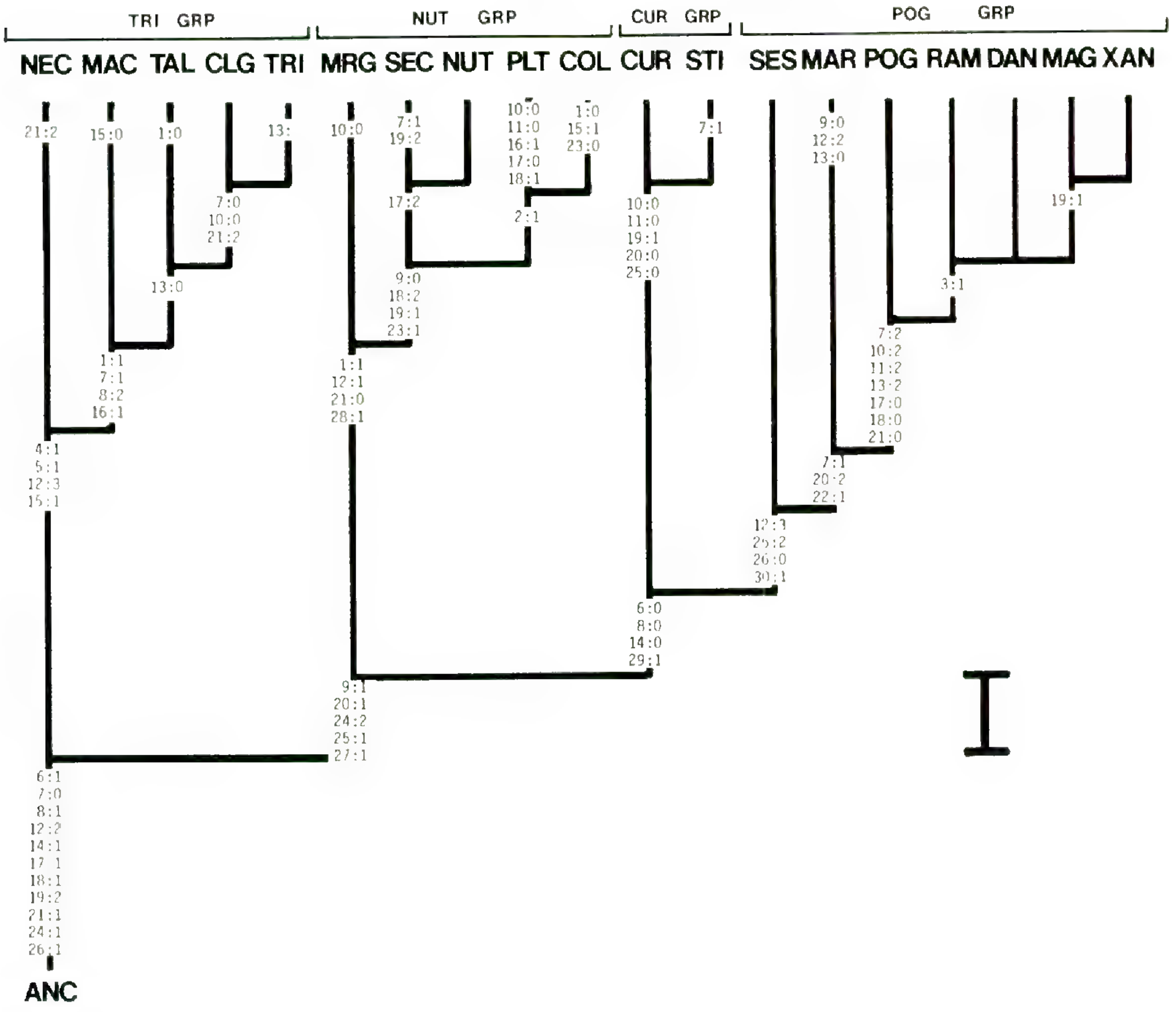


FIGURE 6. Cladogram I. Character-state changes in each lineage given as character number followed by state value. All species have pendent inflorescences. Species groups indicated by horizontal bars above taxa names. (For character states and species abbreviations, see TABLE 6.)

parsimonious cladogram (i.e., with fewer homoplasies) without any alteration in the branching sequence of cladogram I. This revised cladogram (not shown) has eleven fewer homoplasies, six additional synapomorphies (characters 6, 8, 14, 17, 18, 26), and a higher index of consistency (.586). Three characters (7, 19, 21) showed no significant change in homoplasy after the recoding. Although recoding the characters in this fashion does not affect the classification, it does provide new hypotheses on the attributes of the most recent common ancestor of the included pendent species and requires a reevaluation of those character states that are uniquely derived in the various monophyletic lineages. These character-state changes are incorporated into the discussion of monophyletic groups.

MONOPHYLETIC GROUPS. Four primary monophyletic groups or lineages of pendent species are present in both cladograms I and II (FIGURES 6, 7): the *trichocarpa* group (*Heliconia necrobracteata, H. maculata, H. talamancana, H. colgantea,* and *H. trichocarpa*); the *nutans* group (*H. marginata, H. secunda, H. nutans, H. platystachys,* and *H. collinsiana*); the *curtispatha* group (*H.*

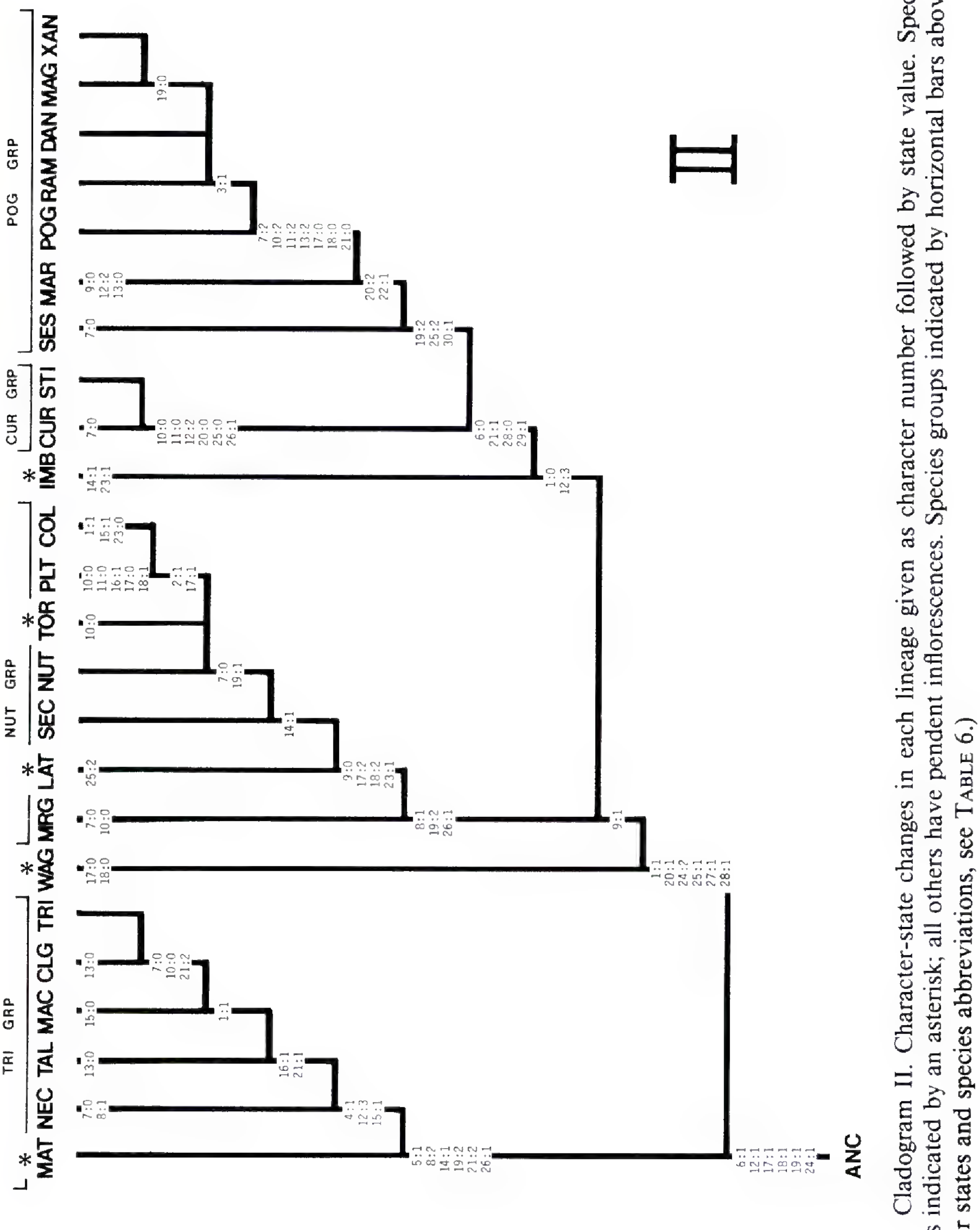


FIGURE 7. Cladogram II. Character-state changes in each lineage given as character number followed by state value. Species with erect inflorescences indicated by an asterisk; all others have pendent inflorescences. Species groups indicated by horizontal bars above taxa names. (For character states and species abbreviations, see TABLE 6.)

curtispatha and *H. stilesii*); and the *pogonantha* group (*H. sessilis, H. mariae, H. pogonantha, H. ramonensis, H. danielsiana, H. magnifica,* and *H. xanthovillosa*).

The five members of the *trichocarpa* group are united with each other and distinguished from other heliconias by several shared derived character states. Oblanceolate leaves that are widest toward the apex and tapering toward the base, shoots that tend to be held in an oblique or a horizontal plane, and a cincinnal bract l/w quotient greater than 2 (except in *Heliconia necrobracteata*) are synapomorphies of this group. Two pollen characters, granulose to minutely spinulose distal-hemisphere sculpturing and indistinct germination apertures, are unique to this group, but they are also present in the hypothetical ancestor shared by all heliconias. These characters are therefore not synapomorphies but do identify members of the group. Staminodes over 1 cm long are nearly unique to members of the *trichocarpa* group (except *H. maculata*) but are also present in *H. collinsiana* of the *nutans* group. Similarly, puberulous to tomentose ovaries are primarily found in the *trichocarpa* group (except *H. necrobracteata*) but are also present in a single species of the *nutans* group, *H. platystachys*.

Synapomorphies of the *nutans* group include slightly curved flowers and pollen with protruding germination apertures. Two characters, cincinnal bracts with a l/w quotient between 1.5 and 2, and pollen grains with a subconvex proximal hemisphere, are primarily restricted to the *nutans* group but are also found in its common ancestor with other heliconias and are therefore not synapomorphies. The *nutans* group is more heterogeneous than the *trichocarpa* group. Although *Heliconia marginata* is united by various apomorphies with the other species in this group, it differs in its involute cincinnal bract margins, in its medium-size euoblate pollen grains lacking constricted distal hemispheres, and in several autapomorphies. *Heliconia marginata* may have closer relatives among South American taxa. *Heliconia collinsiana* and *H. platystachys* are united by the presence of a waxy pseudostem, but each has several states unique within the *nutans* group. *Heliconia collinsiana* has large shoots, long staminodes, and pollen grains without a constriction of the distal hemisphere, states that have evolved independently outside the *nutans* group. *Heliconia platystachys* has pubescent cincinnal bracts and ovaries and large pollen grains—characters unique within the *nutans* group but homoplasious within the genus.

The remaining pendent heliconias are members of the sister *curtispatha* and *pogonantha* groups. Large inflorescences with many cincinnal bracts, a cincinnal bract l/w quotient less than 1.5, anthers connivent within the perianth apex, and pollen grains with sunken germination apertures are character states uniquely derived in the common ancestor of these two groups. The *curtispatha* group has no synapomorphies that distinguish it from all other heliconias but does have several unique states that are absent in its sister *pogonantha* group. For example, puberulous to tomentose cincinnal bracts (inner and outer surfaces) and isopolar pollen grains with convex proximal hemispheres are not unique to the *curtispatha* group but distinguish it from the *pogonantha* group.

Several unique pollen-grain features present in the *pogonantha* group are planar, psilate proximal hemispheres and flattened germination apertures. Two

additional pollen-grain character states, heteropolarity and a truncate distal hemisphere, are synapomorphies of the *pogonantha* group minus *Heliconia sessilis*. This latter species is only loosely united with the other species of this group and may represent a Central American species with closer phylogenetic ties to South American taxa not included in this revision. Similarly, *H. mariae* is the sister species to the remaining taxa of the *pogonantha* group, although it has several features (straight cincinnal-bract margins, parabola-shaped flowers, and puberulous perianth apices) that distinguish it from the other members. A velutinous to woolly vestiture on the rachis, cincinnal bracts (outer and inner surfaces), and perianth apices is a synapomorphy of the remaining species (*H. pogonantha, H. ramonensis, H. danielsiana, H. magnifica,* and *H. xanthovillosa*). Large pollen grains (polar diameter greater than 60 μm and equatorial diameter exceeding 80 μm), an additional shared derived feature of these five species, are also independently derived in *H. platystachys* of the *nutans* group. The *pogonantha* group as a whole is more heterogeneous than either the *curtispatha* or the *trichocarpa* group.

EVOLUTION OF THE INFLORESCENCE HABIT. Evidence from cladogram II (FIGURE 7), which was constructed using the original hypotheses on character polarities (TABLE 6), supports the hypotheses that both pendent and erect inflorescences have most likely evolved several times in *Heliconia* and that pendent heliconias do not constitute a monophyletic group. The five species with erect inflorescences do not form a separate monophyletic lineage but are incorporated into several different lineages of pendent species. Synapomorphies supporting the placement of each erect species are indicated on the cladogram.

Inflorescence habit was not used as a character in the construction of cladogram II. Because the outgroup includes species with both pendent and erect inflorescences, the inflorescence habit of the common ancestor of all heliconias is uncertain. According to cladogram II, if the ancestor had an erect inflorescence, the most parsimonious arrangement of state changes of this character requires five evolutionary steps: either three independent origins of pendent inflorescences and two reversals to the erect state, or two separate origins of the pendent state and three reversals to the erect state. If the ancestor had a pendent inflorescence, then five independent origins of the erect habit are required to map the character on the cladogram most parsimoniously. Regardless of the inflorescence type of the common ancestor, this character is very homoplastic in *Heliconia,* and therefore neither state is homologous in all taxa in which it occurs.

DISCUSSION

Before the present investigation of *Heliconia,* few attempts had been made to analyze the phylogenetic relationships within the entire genus or any part of it. Smith (1968), using less than ten characters, constructed a phylogenetic tree for the Middle American species of *Heliconia,* but provided no methodology or rationale to support his conclusions. All of the species with pendent inflorescences were included in a single lineage that excluded all erect species. Stiles (1979, p. 151) placed 37 Costa Rican species into seven groups based

on morphology and phenology and suggested that these groups may correspond to "real evolutionary or taxonomic relationships." He did not state any explicit method by which he formulated his groups, but his decisions have in part been confirmed by the present analyses. Stiles categorized all of the pendent species into two groups, the *pogonantha* group and the *trichocarpa* group. Stiles's *pogonantha* group, corresponding essentially to the *curtispatha* and *pogonantha* groups defined here, would be monophyletic according to cladogram I. As pointed out earlier, the *curtispatha* group has no states uniquely derived within *Heliconia,* and it could therefore be treated as a sublineage within a more broadly defined *pogonantha* group, as was done by Stiles. However, the set of derived character states present in the *curtispatha* group but absent in the *pogonantha* group supports recognition of the separate taxonomic status of the two lineages. Stiles's second pendent group, the *trichocarpa* group, contains species that are here placed in the *trichocarpa* and *nutans* groups and would therefore be paraphyletic according to cladogram I. *Heliconia marginata,* a somewhat aberrant member of the *nutans* group, was listed as *incertae sedis* by Stiles. He further pointed out that some species with pendent inflorescences (e.g., his *trichocarpa* group—especially *H. secunda*) are very similar to some species with erect inflorescences (e.g., his *tortuosa* group), suggesting that all pendent species should not be classified in a single group or even in closely related groups. This suggestion has been substantiated by cladogram II.

Three of the four pendent monophyletic groups discussed in this revision contain some taxa that are not restricted to Central America (e.g., *Heliconia marginata, H. platystachys, H. curtispatha, H. mariae,* and *H. pogonantha*). In addition, each of the four lineages certainly contains one or more South American species not considered here. The heterogeneity of the *nutans* and *pogonantha* groups is probably due to the fact that some of these species (e.g., *H. marginata, H. platystachys, H. sessilis,* and *H. mariae*), which are quite different from other members of their groups, may have closer relatives in South America than in Central America.

The inclusion of only Central American species requires some caution in the interpretation of the relationships of the taxa in cladograms I and II. However, incorporating pendent South American species or more species with erect inflorescences into the analysis most likely will not require major reinterpretation of the main evolutionary lineages defined here. The addition of more taxa may expand the monophyletic lineages or create new sublineages within the major groups but will not change the relationships among the taxa presently included. For example, *Heliconia mathiasiae,* the sister species of the *trichocarpa* group, has an erect inflorescence and a *Zingiber*-like shoot habit. If other heliconias with *Zingiber*-like shoots were added to the analysis, they would most certainly be placed in the same lineage with *H. mathiasiae.* Taken together, these *Zingiber*-like species would then be the sister group of the *trichocarpa* group. The overall relationships of the other pendent and erect species outside this lineage would not be altered. This reasoning also applies to the inclusion of other species with erect or pendent inflorescences that would be intercalated into the cladogram as sister groups to various species without altering the overall relationships of the other lineages. This was demonstrated here by the incor-

poration of the five species with erect inflorescences in a reanalysis of the pendent species. Neither the relationships of the pendent species nor the circumscription of the four major species groups present in cladogram I was greatly changed in cladogram II by the addition of the extra taxa.

With regard to evolution of inflorescence type, the relatively small number of species included in the cladistic analysis here probably underestimates the degree of homoplasy in this character. An analysis of the entire genus may suggest an even greater number of independent origins of both pendent and erect inflorescences.

Conclusions

The cladistic analyses support the recognition of at least four separate monophyletic lineages of Central American *Heliconia* with pendent inflorescences. The lineages are here called the *trichocarpa* group, the *nutans* group, the *curtispatha* group, and the *pogonantha* group. The first two groups include some species with erect inflorescences as well. These results suggest multiple independent origins of each inflorescence type and therefore argue against the inclusion of all heliconias with pendent inflorescences in a single monophyletic lineage that excludes all species with erect inflorescences.

SPECIES CONCEPTS

The strong physiological isolating mechanisms that in most cases prevent fertilization between species of *Heliconia* (Kress, 1981b, 1983b) would seem to support the biological species concept (Mayr, 1957, 1969). The many sympatric species of the genus that share habitats, flowering times, and pollinators, as well as the few natural hybrids that are produced, suggest severe restrictions on gene flow between species. Even closely related species (e.g., *H. trichocarpa* and *H. colgantea*; *H. curtispatha* and *H. stilesii*) do not hybridize when artificially cross pollinated. Many *Heliconia* species may indeed be "groups of interbreeding natural populations that are reproductively isolated from other such groups" (Mayr, 1969, p. 26). This definition of biological species requires reproductive continuity between populations that is mediated through pollen and/or seed dispersal. Experimental evidence for interpopulational gene flow in any species of *Heliconia* is lacking. In the studies on crossability barriers, only tests between species were attempted and no conclusions have been reached concerning crossability between populations of each taxon. For this reason a biological species concept for *Heliconia* is difficult to accept without resorting to *ad hoc* hypotheses on gene flow.

Simpson (1961) and Wiley (1978, 1981) have suggested a species concept that does not rely exclusively on reproductive continuity between populations of a species but does accept it as an important component of species cohesion. The evolutionary species is "a lineage of ancestor-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate" (Wiley, 1981, p. 25). A lineage consists of one or more populations that share a common history of descent not shared

by other populations. Identity is interpreted as the assemblage of morphological (and behavioral) characters that permits "recognition" between organisms. Reproductive isolation may of course be necessary for maintenance of the genetic identity of an evolutionary species. However, morphological coherence of any species, especially one that is distributed over large geographic areas, is more likely a consequence of genealogy than of gene flow between its members.

Boundaries between species of *Heliconia* were defined by morphological, ecological, and geographic discontinuities. Botanists have variously advocated narrow and broad concepts when awarding species status to recognized taxonomic entities of *Heliconia.* Actually, the taxonomic rank designated by the taxonomist may be of little importance in understanding the biology of the organisms. The duty of the systematist is to document the extent of natural variation, record the levels of discontinuities, and define monophyletic groups. In the present study of *Heliconia,* differences in color, size, and shape of sexual reproductive structures that have been observed in the field have been given high priority in making taxonomic decisions. Assemblages of individuals sharing distinctive cincinnal-bract and flower characteristics that appear to affect pollinator visitation are awarded species status. These morphological characteristics are always correlated with geographic discontinuities. Varietal status is accepted for assemblages of individuals showing minor morphological distinction and allopatric distributions. Taxonomic inflation has been avoided where possible, but not at the expense of obscuring information that is indispensible to other biological investigations.

MATERIALS AND METHODS

The relatively few taxonomic studies of *Heliconia* and the lack of any recent comprehensive revision of the genus are in part due to the difficulties of preparing representative herbarium specimens. Although usually quite common in the Neotropics, heliconias are poorly collected because of their large stature and their fleshy nature, and collections that are made are often unimpressive and uninformative. In preparing the present revision, I have emphasized extensive work with living plants in the field; I have seen all of the taxa described here and have studied them in their natural habitats. Morphological data for the taxonomic descriptions, diagnostic keys, and phylogenetic analysis have been taken from living plants *in situ,* and voucher specimens are deposited in the Duke University Herbarium (DUKE). From one (for the rarer taxa) to seven populations (for the more widely distributed taxa) have been sampled for each taxon (see TABLE 5). Three or more genetically different individuals have been included in each population sample.

In addition to the field studies, numerous specimens from various herbaria (A, BM, CR, DUKE, F, GB, GH, K, M, MO, NY, PMA, S, SCZ, U, UC, US, and W) have been examined. Information from these specimens has been used to supplement field observations on morphology, habitat, geographic distribution, and phenology.

TAXONOMIC TREATMENT

Heliconia L. Mant. Pl. **2:** 147. 1771, nom. cons. TYPE SPECIES: *Heliconia bihai* (L.) L.

Bihai Miller, Gard. Dict. abr. ed. 4. Vol. 1 [alph. order]. 1754, nom. rejic.
Bihai Adanson, Fam. Pl. Pt. 2. 67. 1763, nom. rejic.
Heliconiopsis Miq. Fl. Indiae Batavae **3:** 590. 1855. TYPE SPECIES: *Heliconiopsis amboinensis* Miq.
Bihaia Kuntze, Rev. Gen. Pl. **2:** 684. 1891, orth. var.

Medium to large rhizomatous herbs with *Musa*-, *Canna*-, and *Zingiber*-like habits, forming clones with erect, leafy shoots in groups of few (1 or 2) to many (>50). Pseudostem composed of overlapping sheathing leaf bases of various colors and textures. Leaves usually large, either distichous with all blades lying in a single plane or appearing spirally arranged; petiole short (*Zingiber*-like), medium length (*Canna*-like), or long (*Musa*-like); blade with the base usually unequal on 2 sides of midrib, cordate to attenuate, the upper surface usually green, the lower surface green to maroon. Inflorescence terminal on leafy or leafless shoot, erect, pendent, or nodding, consisting of brightly colored peduncle, rachis, and few (3 to 5) to many (>30) cincinnal bracts; cincinnal bracts distichous or spirally arranged, each subtending cincinnus of few (3) to many (>40) flowers. Flowers hermaphroditic, each subtended by opaque or membranous, variously colored floral bract, persistent or decomposing after anthesis; pedicel short (5 mm) to long (2 cm); perianth consisting of 2 whorls united at base with various degrees of fusion within and between whorls, the calyx with 2 free abaxial sepals adnate to corolla except at apex, and 1 nearly free adaxial sepal usually reflexed at anthesis, the corolla with 3 petals, connate except for free margins opposite free sepal; pollen-bearing stamens 5, the filaments long, linear, attached to base of perianth tube, the anthers 4-loculate, linear, situated at apex of perianth at anthesis, dehiscence longitudinal; pollen large, pseudoinaperturate, oblate to spheroidal, heteropolar with reduced surface ornamentation; staminode 1, opposite free sepal, varying in size and shape; ovary inferior, 3-celled, the ovules solitary, erect, the style filiform, straight, or geniculate, the stigma capitate or lobed. Fruits 1- to 3-seeded drupes, usually blue. Seeds surrounded by stony, roughened endocarp, exarillate; embryo straight; endosperm copious.

KEY TO CENTRAL AMERICAN SPECIES OF HELICONIA WITH PENDENT INFLORESCENCES

The following key was constructed from living plants and hence is most useful in the field. If sufficient label data are supplied on herbarium sheets, however, the key can be used to identify dried specimens as well. Some characters (e.g., pollen-grain features) will be of limited diagnostic value to most workers, but they are included for completeness. The key is based primarily on the phylogenetic tree (FIGURE 6) and is therefore a "natural" one that reflects the phylogenetic history of the taxa. Members of each of the four species groups

(*trichocarpa, nutans, curtispatha,* and *pogonantha* groups) are placed together in adjacent entries.

A. Inflorescences small (< 20 cincinnal bracts); cincinnal bract l/w > 1.4; anthers flared outside perianth apex; pollen germination apertures indistinct or distinctly protruding but not sunken.
B. Shoots oriented horizontally or obliquely; leaves oblanceolate, widest toward apex and tapering toward base; flowers sigmoid; pollen germination aperture indistinct.
C. Cincinnal bract l/w < 2; ovaries glabrous. . . . . 1. *H. necrobracteata.*
C. Cincinnal bract l/w > 2; ovaries puberulous to villous.
D. Rachis and floral bracts usually glabrous; perianth green or yellow-green, slightly sigmoid; staminode apex acuminate or apiculate.
E. Shoots < 3 m in height; pseudostem pale green with dark brown spots; cincinnal bracts red, becoming green distally; perianth glabrous, yellow, becoming green distally. . . . . 2. *H. maculata.*
E. Shoots usually > 3 m in height; pseudostem green; cincinnal bracts mostly green; perianth puberulous, mostly green. . . . . 3. *H. talamancana.*
D. Rachis and floral bracts puberulous to tomentose; perianth yellow, strongly sigmoid; staminode apex bilobed.
F. Cincinnal bracts bright pink, often becoming green toward apex, puberulous; floral bracts stiff, conspicuous; perianth puberulous. . . . . 4. *H. colgantea.*
F. Cincinnal bracts red, often becoming maroon toward apex, glabrous; floral bracts soft, inconspicuous; perianth glabrous. . . . . 5. *H. trichocarpa.*
B. Shoots usually erect; leaves oblong-elliptic, widest in middle; flowers only slightly curved; pollen germination aperture distinct and protruding.
G. Shoots < 3 m in height; pseudostem and lower surface of leaf blade usually not glaucous.
H. Habitat aquatic; leaves held stiffly erect; cincinnal bracts red and yellow, margins involute at base; staminode apex apiculate; pollen with distal hemisphere lacking constrictions. . . . . 6. *H. marginata.*
H. Habitat terrestrial; leaves not held stiffly erect; cincinnal bracts entirely red, margins straight to revolute at base; staminode apex trilobed; pollen with distal hemisphere having constrictions.
I. Rachis glabrous, extremely twisted, making inflorescence appear very contorted; perianth length 5–6 cm. . . . . 7. *H. secunda.*
I. Rachis puberulous to tomentose, sometimes twisted so that all cincinnal bracts oriented on one side of inflorescence; inflorescence usually not highly contorted; perianth length 4–5 cm. . . . . 8. *H. nutans.*
G. Shoots > 3 m in height; pseudostem and lower surface of leaf blade usually glaucous.
J. Cincinnal bracts red and yellow; floral bracts puberulous; ovaries puberulous to tomentose. . . . . 9. *H. platystachys.*
J. Cincinnal bracts entirely red; floral bracts glabrous; ovaries glabrous. . . . . 10. *H. collinsiana.*

A. Inflorescences large (> 20 cincinnal bracts); cincinnal bract l/w < 1.4; anthers convent within perianth apex; pollen germination aperture distinct but sunken.
K. Peduncle, rachis, and cincinnal bracts essentially glabrous; flowers parabolic or only slightly sigmoid; perianth essentially glabrous, sometimes slightly puberulous at apex; pollen with distal hemisphere not truncate.
L. Cincinnal bracts not imbricate, l/w > 0.8; perianth yellow.
M. Habitat terrestrial; lamina base truncate to cordate; peduncle long, inflo-

rescence thus distinctly pendent; cincinnal bract l/w 1.1–1.3; flowers parabolic.

N. Rachis slightly flexuose; cincinnal bracts distichous to spirally arranged, alternate bracts distant and not touching. . . . . 11. *H. curtispatha.*

N. Rachis very flexuose; cincinnal bracts strictly distichous, alternate bracts often touching or overlapping. . . . . 12. *H. stilesii.*

M. Habitat aquatic; lamina base attenuate; peduncle very short, obscure, inflorescence thus sessile and nodding to pendent; cincinnal bract l/w < 1; flowers slightly sigmoid. . . . . 13. *H. sessilis.*

L. Cincinnal bracts imbricate, l/w < 0.9; perianth red to pink. 14. *H. mariae.*

K. Peduncle, rachis, and/or cincinnal bracts usually densely velutinous to woolly, in some cases all or some parts of inflorescence glabrous; flowers strongly sigmoid; perianth apex densely velutinous; pollen with distal hemisphere truncate.

O. Peduncle, rachis, and cincinnal bracts essentially glabrous.

P. Peduncle and rachis red or yellow, cincinnal bracts entirely red or red and yellow; floral bracts and perianth with golden hairs. . . . . 15. *H. pogonantha.*

P. Peduncle, rachis, and cincinnal bracts rose-red; floral bracts and perianth with bright yellow hairs. . . . . 16. *H. ramonensis.*

O. Peduncle, rachis, and/or cincinnal bracts densely velutinous to woolly.

Q. Cincinnal bracts bichromatic, red and yellow, velutinous. . . . . 15. *H. pogonantha.*

Q. Cincinnal bracts monochromatic, not red and yellow, velutinous to woolly.

R. Inflorescence orange to rose-red, with orange hairs; perianth with orange or buff to rusty orange hairs.

S. Inflorescence pink to rose-red, with rusty orange hairs; perianth with rusty orange hairs. . . . . 16. *H. ramonensis.*

S. Inflorescence orange-red with orange (fresh) or buff (dried) hairs. . . . . 17. *H. danielsiana.*

R. Inflorescence burgundy with golden to burgundy hairs or yellow with yellow hairs; perianth with golden or yellow hairs.

T. Inflorescence deep red to burgundy, with golden to burgundy hairs; perianth with golden hairs. . . . . 18. *H. magnifica.*

T. Inflorescence bright yellow-green with yellow hairs; perianth with bright yellow hairs. . . . . 19. *H. xanthovillosa.*

1. **Heliconia necrobracteata** Kress, J. Arnold Arbor. **62:** 248. 1981. TYPE: Panama, Coclé, 6 mi beyond El Valle de Antón, behind Cerro Gaital, elev. 900 m, *Kress, Clarkson, & McDade 77-842* (holotype, DUKE!; isotypes, K!, MO!). FIGURE 8; PLATE I, A, B.

Herb with *Musa*-like habit, 4–4.5 m tall. Leafy shoots in groups of 3 to 12; pseudostem dull gray-green with brown spots, glabrous, 1–2 m tall, 4–6.5 cm in diameter; leaves 3 to 5 per shoot, all tending to lie in horizontal plane; longest petiole olive green, glabrous, 65–100 cm long, 1.5–2 cm in diameter; blade oblanceolate, widest toward acute to obtuse apex, the base unequal, attenuate along petiole, the upper surface dark green, glabrous, with midrib light green and glabrous, the lower surface gray-green, glabrous, with midrib yellow-green and glabrous, the longest blade 1.9–2.4 m by 25–35 cm. Inflorescence pendent, 40–55 cm long; peduncle red, glabrous to puberulous, 25–35 cm long, 1.3–1.8 cm in diameter; rachis flexuose, dark red, puberulous, 1–

1.4 cm in diameter at base; cincinnal bracts spirally arranged, 10 to 20 per inflorescence, oriented 135–140° to axis of inflorescence, becoming more reflexed with age, the basal bract usually fertile, the middle bract with apex acuminate, margins straight, inner surface yellow (sometimes with red margins) and glabrous, outer surface red and glabrous to puberulous, 12–17 cm long, 7–8 cm wide at base, l/w = 1.9, all bracts becoming necrotic soon after anthesis, deteriorating distally first and basipetally with age. Floral bracts more or less translucent at anthesis, quickly decomposing, white, puberulous to velutinous along abaxial margins, 3.5–4.5 cm long, 1.5–2 cm wide at base. Flowers 8 to 13 per cincinnus; pedicel pale yellow, tomentose, 1.4–2.2 cm long; perianth yellow to deep yellow, glabrous, puberulous along margins, 4.5–5 cm long, 6–9 mm wide at base, at anthesis curved 50–80° and sigmoid; free sepal reflexed, fused sepals with apices slightly reflexed; staminode white, 1.5–2 cm by 4–5 mm, apex bilobed; stamens with anthers partially flared outside of apex of corolla tube; pollen *trichocarpa* type, medium size (54 × 74 μm), euoblate (P/E = 0.72), isopolar (DR/PR = 1.02), with the distal hemisphere planar, minutely spinulose, the proximal hemisphere convex, minutely spinulose to granulose, the germination aperture indistinct; ovary pale yellow, glabrous, 5–6 by 6–7 mm. Drupes glabrous.

SPECIMENS EXAMINED. **Panama.** COCLÉ: base of three peaks beyond El Valle de Antón, elev. 800 m, *Kress & Cooper-Smith 76-652* (DUKE); behind Cerro Gaital, elev. 2200 ft, *Kress et al. 80-1158* (DUKE), elev. 2400 ft, *Kress & Hammel 83-1583* (DUKE); mtns. above El Valle, in forest on Sr. Furlon's Finca, *Stimson 5037* (SCZ), *5038* (SCZ).

PHENOLOGY. Flowering early in rainy season (April) through late August.

HABITAT AND DISTRIBUTION. This species is found on steep, forested slopes at elevations of 650–1000 m in the region of El Valle de Antón in Panama (MAP 1). As more collections are made in the provinces of Coclé and Veraguas, especially on the Atlantic slopes, the known distribution will probably be broadened.

RELATIONSHIPS. *Heliconia necrobracteata,* a member of the *trichocarpa* group, is distinctive in its glabrous ovaries, its stouter vegetative shoots and inflorescences, and its red cincinnal bracts that decompose and turn black even while flowers are still being produced.

2. **Heliconia maculata** Kress, J. Arnold Arbor. **62**: 244. 1981. TYPE: Panama, Colón, along Río Guanche, 1 km from road to Portobelo, elev. ca. 8 m, *Kress & Knapp 80-1240* (holotype, DUKE!; isotypes, F!, GH!, K!, MO!, PMA!). FIGURE 9; PLATE I, C, D.

Herb with *Musa*-like habit, 2–2.5 m tall. Leafy shoots congested, in groups of 3 to 25; pseudostem pale greenish gray with distinctive dark brown spots throughout, glabrous, 1.2–1.7 m tall, 2.2–2.5 cm in diameter; leaves 6 per shoot, all tending to lie in horizontal plane; petiole olive green, glabrous, 22–34 cm long, 8–10 mm in diameter; blade oblanceolate, widest toward acute apex, the base unequal, attenuate, extending along petiole, the upper surface green, glabrous, with midrib light green and glabrous, the lower surface gray-green, glabrous, with midrib yellow and glabrous to slightly scurfy, the longest

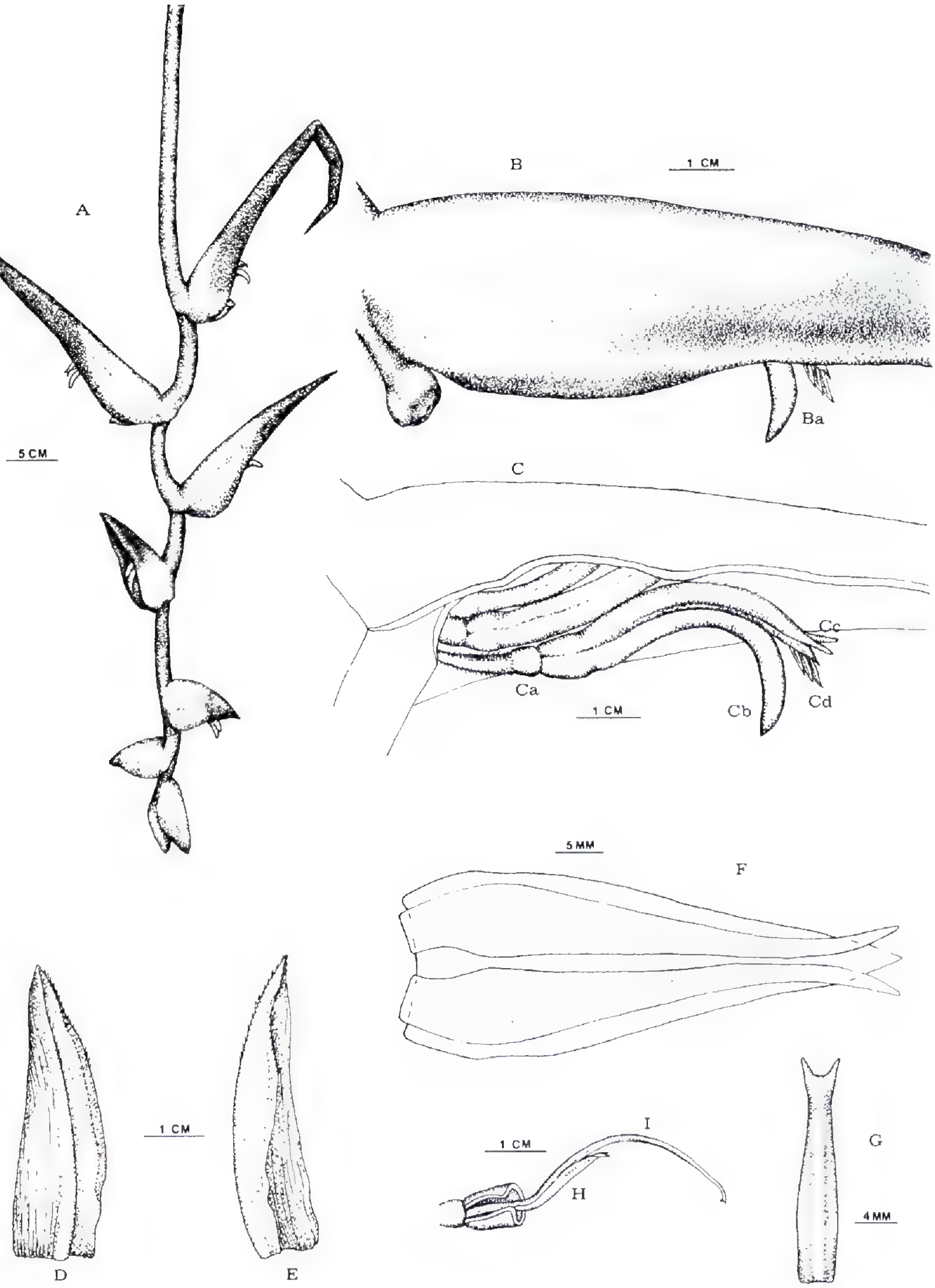
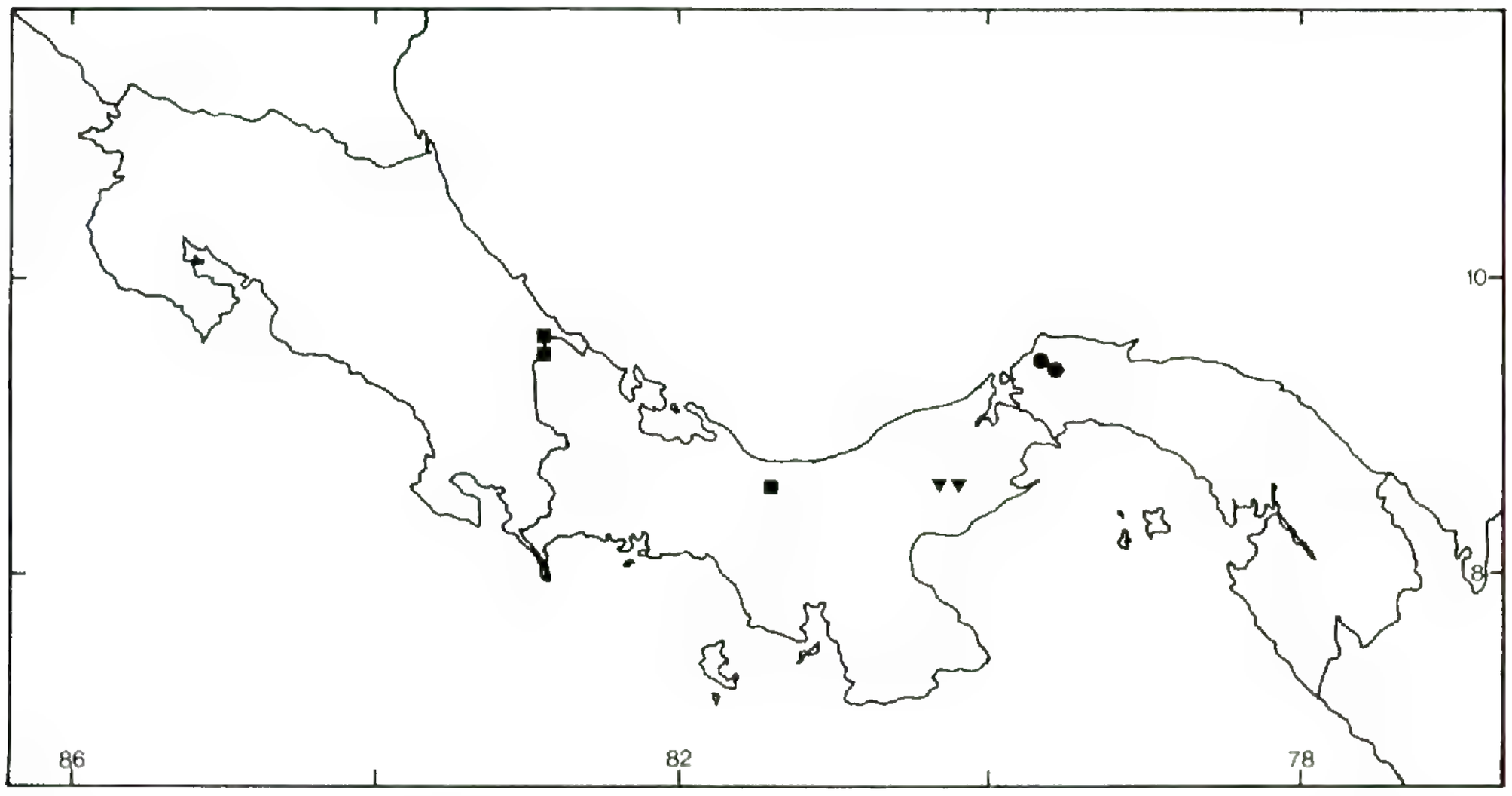


FIGURE 8. *Heliconia necrobracteata*. A, inflorescence. B, C, cincinnal bracts: B, entire (Ba, flower protruding at anthesis); C, cut-away, floral bracts removed showing flower at anthesis (Ca, ovary; Cb, free sepal; Cc, fused sepals, slightly reflexed; Cd, anthers, partially exserted). D, E, floral bracts: D, abaxial view; E, lateral view. F, perianth, outer surface showing 2 sepals fused to partially spread-open corolla tube. G, H, staminode: G, abaxial view; H, position relative to style, lateral view. I, style and stigma.

blade 1.1–1.3 m by 24–26 cm. Inflorescence pendent, to 51 cm long; peduncle green and dark maroon, glabrous, 7–32 cm long, 1 cm in diameter; rachis flexuose, dull red, glabrous to slightly puberulous, 7–8 mm in diameter at base; cincinnal bracts spirally arranged, 7 or 8 per inflorescence, oriented 90° to axis



MAP 1. Costa Rica and Panama, showing allopatric distribution of *Heliconia necrobracteata* (triangles), *H. maculata* (circles), and *H. talamancana* (squares).

of inflorescence, the basal bract fertile or sterile, the middle bract with apex long-acuminate, margins straight becoming somewhat flared at base, inner surface pale orange and glabrous, outer surface red basally becoming green toward apex and glabrous, 14–17 cm long, 4–4.5 cm wide at base, l/w = 3.7. Floral bracts translucent at anthesis, quickly decomposing, cream, glabrous to puberulous abaxially, 4–5 cm long, 1.1–1.4 cm wide at base. Flowers 15 to 20 per cincinnus; pedicel pale yellow, pubescent to hirsute, 1–1.5 cm long; perianth yellow basally, green at apex, glabrous to slightly puberulous, 5 cm long, 1 cm wide at base, at anthesis curved 30–50° and slightly sigmoid; free sepal slightly reflexed, fused sepals with apices not reflexed; staminode white, 7–10 by 3 mm, apex apiculate; stamens with anthers flared outside perianth apex; pollen *trichocarpa* type, medium size (49 × 67 μm), euoblate (P/E = 0.73), isopolar (DR/PR = 0.97), the distal hemisphere subconvex, verrucose, the proximal hemisphere convex, granulose, the germination aperture indistinct; ovary white, pubescent, 4–5 by 6 mm. Drupes glabrous to puberulous, 8 by 9 mm; pyrenes 6 by 5 mm.

SPECIMENS EXAMINED. **Panama.** COLÓN: Río Guanche, forest, elev. ca. 50 ft, *Maas et al. 1583* (F, MO); in forest 3–7 km from bridge, elev. 300–700 ft, *Hammel et al. 4899* (MO); *Knapp 1020* (MO), *1422* (MO); below Cerro Bruja along Río Escondaloso, elev. 100–200 m, *Kress & Knapp 82-1406* (DUKE).

PHENOLOGY. Flowering late July through early October.

HABITAT AND DISTRIBUTION. This species occurs at lower elevations along stream banks and in adjacent understory of primary forest. It will invade more open areas (often created by man), where it generally produces more shoots per clump. So far, *Heliconia maculata* has been collected at only two localities in Colón Province, Panama (MAP 1); as more collections are made, it will probably be found in other forested areas in the Atlantic coastal forests of Panama.

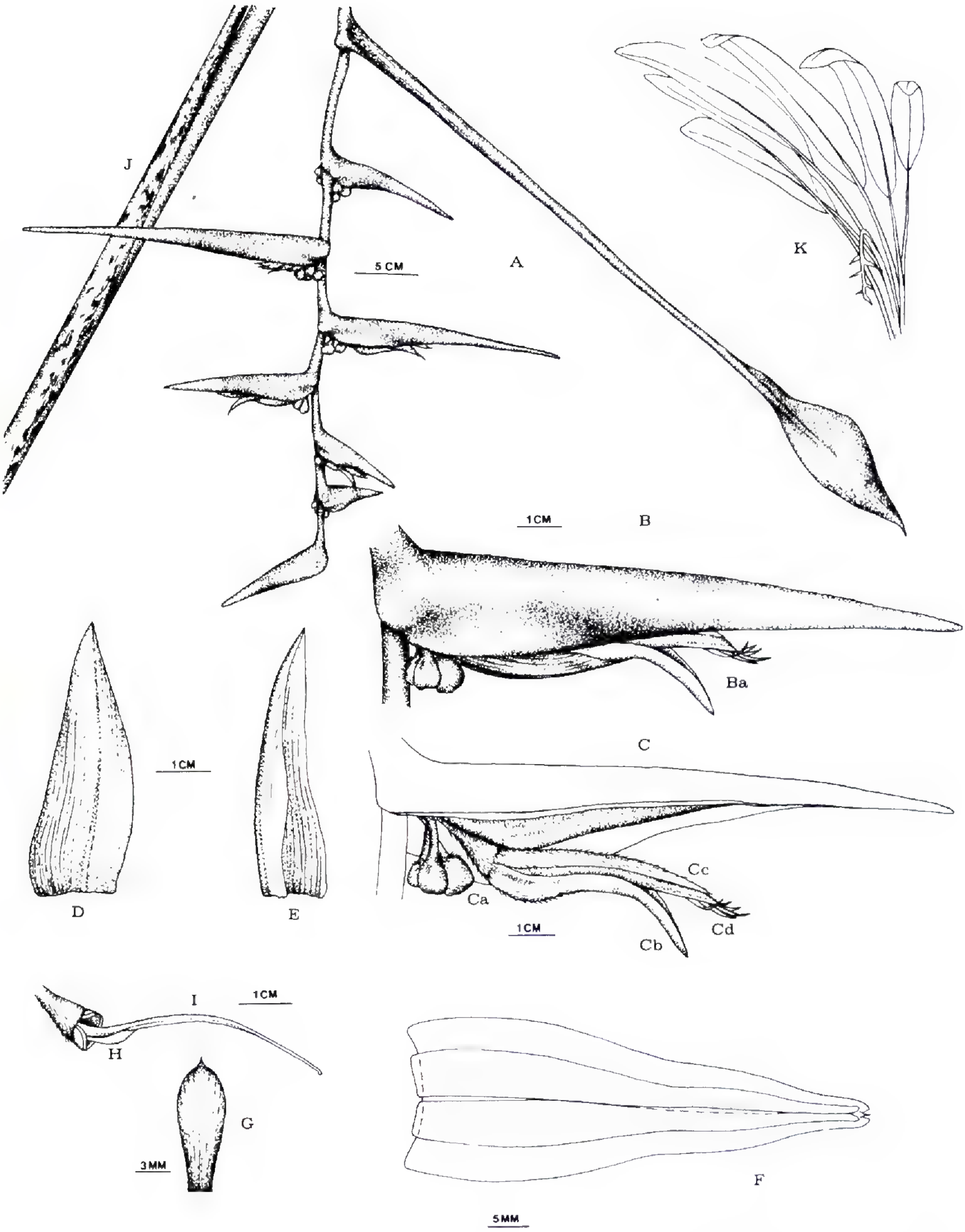


FIGURE 9. *Heliconia maculata*. A, inflorescence. B, C, cincinnal bracts: B, entire (Ba, flower protruding at anthesis); C, cut-away, floral bracts removed showing flower at anthesis (Ca, ovary; Cb, free sepal; Cc, fused sepals, not reflexed; Cd, anthers, exserted). D, E, floral bracts: D, abaxial view; E, lateral view. F, perianth, outer surface showing 2 sepals fused to partially spread-open corolla tube. G, H, staminode: G, abaxial view; H, position relative to style, lateral view. I, style and stigma. J, pseudostem. K, vegetative habit.

RELATIONSHIPS. Several pollen characters, as well as the distinctive pubescent ovaries and the obliquely or horizontally oriented leaf blades that are widest near the apex, ally this species with other members of the *trichocarpa* group. However, it differs from the other species in its dark brown–spotted pseudostem (also present in *Heliconia necrobracteata*), its red and green cincinnal bracts, and its yellow and green, glabrous perianths.

3. **Heliconia talamancana** Daniels & Stiles, Brenesia **15**(Supl.): 42. 1979. TYPE: Costa Rica, [Limón,] on ridge W of BriBrí, elev. 200 m, *Daniels, Stiles, & Kress 115* (holotype, F!; isotypes, CR, US). PLATE I, E, F.

Herb with *Musa*-like habit, 4–4.5 m tall. Leafy shoots in groups of 5 to 15; pseudostem green, glabrous, 2.2–2.6 m tall, 3.5–4 cm in diameter; leaves 5 per shoot, all tending to lie in horizontal plane; petiole olive green, glabrous, 85–100 cm long, 1.5–1.6 cm in diameter; blade oblanceolate, widest toward obtuse apex, the base unequal, attenuate along petiole, the upper surface green, glabrous, with midrib green and glabrous, the lower surface gray-green, glabrous, with midrib green-yellow and glabrous, the longest blade 2.1–2.5 m by 32–35 cm. Inflorescence pendent, to 65 cm long; peduncle green, glabrous, 6–27 cm long, 1.3–1.5 cm in diameter; rachis flexuose, green and red, glabrous, 1.2–1.4 cm in diameter at base; cincinnal bracts spirally arranged, 8 to 13 per inflorescence, oriented 90° to axis of inflorescence, the basal bract usually fertile, the middle bract with apex long-acuminate, margins straight, inner surface white to green and glabrous, outer surface green becoming red at rachis and glabrous, 17–20 cm long, 6–7 cm wide at base, l/w = 2.9. Floral bracts opaque, decomposing after anthesis, white, glabrous to puberulous abaxially, 5–5.3 cm long, 1.5–2 cm wide at base. Flowers 15 to 20 per cincinnus; pedicel white, tomentose, 1.3–1.6 cm long; perianth white, green apically, puberulous, 5–5.2 cm long, 1 cm wide at base, at anthesis curved 30–40° and slightly sigmoid; free sepal reflexed, fused sepals with apices not reflexed; staminode white, spatulate, 1.1 cm by 3 mm, apex apiculate; stamens with anthers partially flared outside corolla tube; pollen *trichocarpa* type, medium size (53 × 72 μm), euoblate (P/E = 0.74), isopolar (DR/PR = 0.95), with the distal hemisphere subconvex to planar, verrucose to granulose, the proximal hemisphere convex, verrucose to granulose, the germination aperture indistinct; ovary white, villous, 6–8 by 7–8 mm. Drupes puberulous, 1–1.2 by 1.2–1.5 cm.

SPECIMENS EXAMINED. **Costa Rica.** LIMÓN: 1–3 km N of BriBrí, Río Sixaola Drainage, elev. 20–200 m, *Burger & Antonio 11000* (F); in hills above BriBrí, elev. ca. 250 m, *Kress et al. 76-625* (DUKE), elev. ca. 800 ft, *Kress et al. 77-791* (DUKE). **Panama.** VERAGUAS: along road on Pacific slope, 1–3 km above Escuela Agrícola Alto Piedra, elev. 700–800 m, *Croat 25997* (MO).

PHENOLOGY. Flowering June to October.

HABITAT AND DISTRIBUTION. This species is distributed on the Caribbean slopes from the Río Sixaola in Limón, Costa Rica, to Veraguas, Panama (MAP 1). It is most often found on steep, wooded slopes in primary and old secondary growth at elevations up to 700 m.

RELATIONSHIPS. *Heliconia talamancana* is closely related to *H. maculata* and other species in the *trichocarpa* group. It differs from *H. maculata* in its greater overall stature (> 3 m), its essentially green cincinnal bracts, and its green, pubescent perianth.

4. **Heliconia colgantea** R. R. Smith ex Daniels & Stiles, Brenesia **15**(Supl.): 18. 1979. TYPE: Costa Rica, [Puntarenas,] 10 km ENE of Palmar Norte, *Burger & Matta 4662* (holotype, F!; isotypes, CR!, GH!, NY!, US!).

PLATE II, A, C.

Herb with *Musa*-like habit, 2 m tall. Leafy shoots solitary or in pairs; pseudostem yellow-green, glabrous, 90–125 cm tall, 2.2–2.7 cm in diameter; leaves 6 per shoot, all fanning out from pseudostem and tending to lie in horizontal plane; petiole green to dark green, glabrous, 34–45 cm long, 9–11 mm in diameter; blade oblanceolate, widest toward obtuse apex, the base unequal, obtuse to attenuate along petiole, the upper surface dark green, glabrous, with midrib dark green and glabrous, the lower surface gray-green, glabrous, with midrib green and glabrous, the longest blade 1.1–1.3 m by 20–25 cm. Inflorescence pendent, to 45 cm long; peduncle red with green striations, puberulous, 14–17 cm long, 1–1.2 cm in diameter; rachis flexuose, pink-red, puberulous to tomentose, 9–10 mm in diameter at base; cincinnal bracts spirally arranged, 8 to 10 per inflorescence, oriented 120–165° to axis of inflorescence, becoming more reflexed with age, the basal bract usually fertile, the middle bract with apex acuminate, margins straight becoming somewhat revolute near rachis, inner surface yellow and pink and glabrous, outer surface pink becoming green toward apex and puberulous, 19–22 cm long, 7–8 cm wide at base, l/w = 2.7. Floral bracts translucent, persistent, conspicuous, pale yellow, stiff, puberulous abaxially, 3.5–4.2 cm long, 8–10 mm wide at base. Flowers 15 to 20 per cincinnus; pedicel pale yellow, puberulous to tomentose, 1–1.2 cm long; perianth yellow, densely puberulous, 5.1–5.5 cm long, 8–9 mm wide at base, at anthesis curved 50–70° and sigmoid; free sepal reflexed, fused sepals with apices sometimes slightly reflexed; staminode white, 1–1.1 cm by 2–3 mm, apex bidentate; stamens with anthers flared outside perianth apex; pollen *trichocarpa* type, medium size (55 × 79 μm), euoblate (P/E = 0.69), isopolar (DR/PR = 0.88), with the distal hemisphere planar, minutely spinulose, the proximal hemisphere convex, minutely spinulose to granulose, the germination aperture indistinct; ovary pale yellow, puberulous to tomentose, 4–6 by 6–7 mm. Drupes sparsely tomentose.

SPECIMENS EXAMINED. **Costa Rica.** PUNTARENAS: forested hills near Palmar Norte, elev. 300 m, *Allen 6551* (F, PMA); 10 km N of Palmar Norte along Pan Am Hwy., elev. ca. 100 m, *Kress et al. 76-595* (DUKE), *77-878* (DUKE); cult. at Las Cruces Trop. Bot. Garden, San Vito de Java, elev. 3900 ft, *Kress 78-1027* (DUKE). **Panama.** CHIRIQUÍ: Burica Peninsula, 10–11 mi W of Puerto Armuelles in vic. of San Bartolo Limite, elev. 300–500 m, *Croat 21994* (F). DARIÉN: Río Pucuro between Cerro Mali and Cerro Tacarcuna, Río Pucuro base camp, elev. 650 m, *Gentry & Mori 13877* (MO); E slope of Cerro Sapo, elev. 2500 ft, *Hammel 1275* (MO); Río Pirre, near Dos Bocas, *Foster & Augsburger 2844* (F); Cerro Pirre, *Bristan 628* (NY), *629* (NY); 4.5 km S of El Real, moist forest at base of foothills of N slope of Cerro Pirre, *Mori & Kallunki 5413* (GB, MO); headwaters of Río

Tuquesa, vic. of gold-mining camp of Tyler Kittredge, *Croat 27198* (MO); 10 km NE of Jaqué, Río Pavarando, elev. 1400 ft, *D'Arcy & Sytsma 14522* (MO), *Sytsma & D'Arcy 3375* (MO); Río Jaqué valley, elev. 300–500 m, *Knapp & Mallet 3085* (MO). PANAMÁ: S of Ipetí, Serranía de Majé, elev. 450–600 m, *Knapp et al. 4553* (MO).

PHENOLOGY. Flowering mainly January to September.

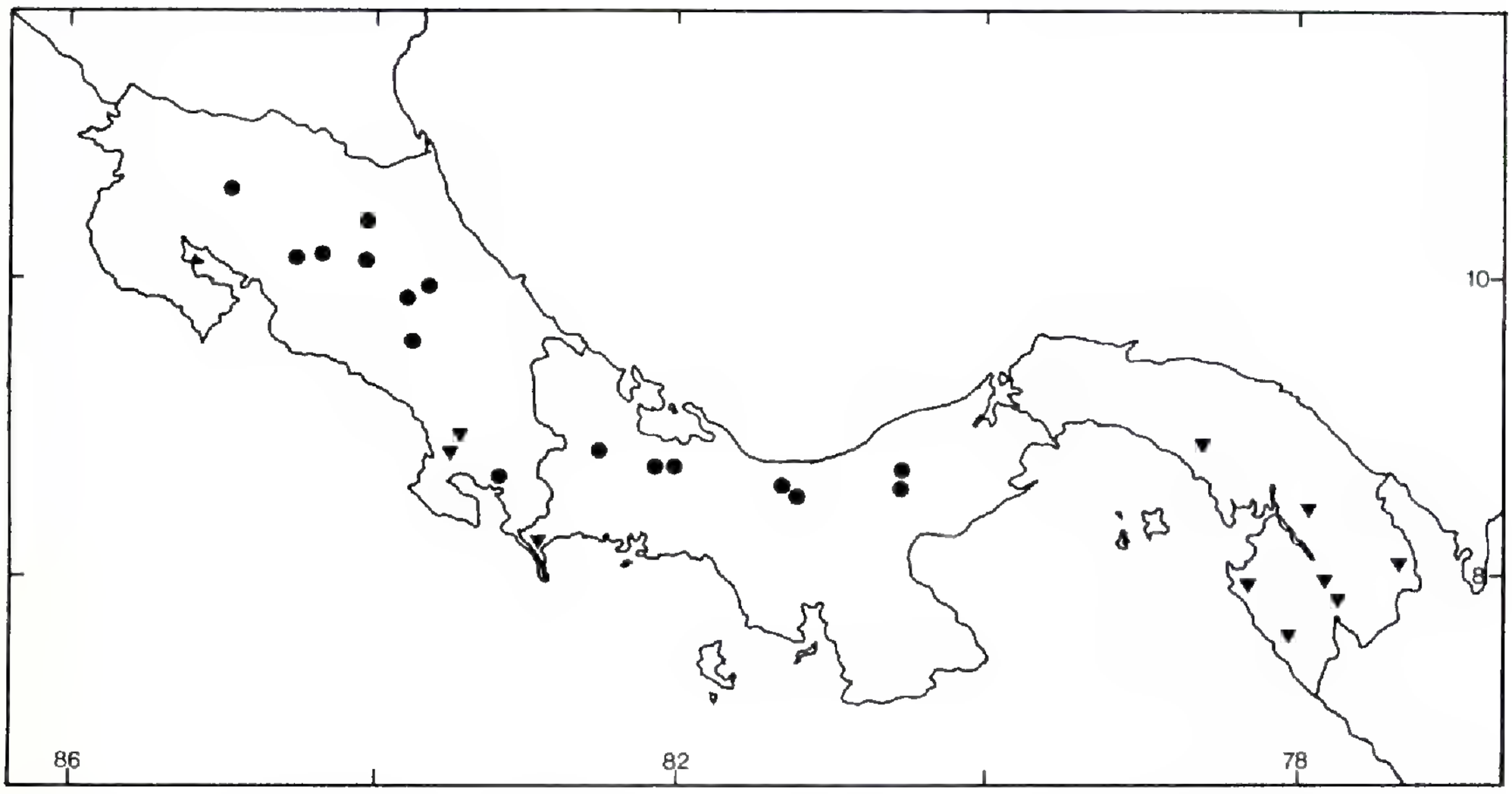
HABITAT AND DISTRIBUTION: *Heliconia colgantea* has been found in several localities in Costa Rica and Panama (MAP 2). It is restricted mainly to moist or wet forested slopes and ravines between 100 and 800 m.

RELATIONSHIPS. This species is a member of the *trichocarpa* group. Slightly pubescent, bright pink cincinnal bracts with green apices, a puberulous perianth, and stiff, conspicuous floral bracts distinguish *Heliconia colgantea* from its closest relative, *H. trichocarpa*.

5. **Heliconia trichocarpa** Daniels & Stiles, Brenesia **15**(Supl.): 44. 1979. TYPE: Costa Rica, Alajuela, La Balsa area N of San Ramón, elev. 800 m, *Daniels, Kress, & Hutchison 112* (holotype, F!; isotypes, CR, US). PLATE II, B, D.

H. trichocarpa var. *caducispatha* Daniels & Stiles, Brenesia **15**(Supl.): 44. 1979. TYPE: Costa Rica, Puntarenas, 42 km S of Palmar Norte along Interamerican Hwy., elev. 100 m, *Daniels & Stiles 129* (holotype, F!; isotypes, CR, US).

Herb with *Musa*-like habit, 2–4 m tall. Leafy shoots in groups of 4 to 20; pseudostem green (sometimes with red), glabrous, 80–190 cm tall, 2–4 cm in diameter; leaves 4 to 6 per shoot, all tending to lie in horizontal plane; petiole green to olive green, glabrous, 35–90 cm long, 7–13 mm in diameter; blade oblanceolate, widest toward acute to obtuse apex, the base unequal, obtuse to attenuate along petiole, the upper surface green to dark green, glabrous, with midrib light green to olive green and glabrous, the lower surface gray-green, glabrous, with midrib yellow-green and scurfy, the longest blade 85–175 by 17–30 cm. Inflorescence pendent, to 60 cm long; peduncle red to rose-red, puberulous, 10–50 cm long, 1–1.8 cm in diameter; rachis flexuose, red, puberulous, 6–11 mm in diameter at base; cincinnal bracts spirally arranged, 6 to 10 per inflorescence, oriented 110–150° to axis of inflorescence, the basal bract usually fertile, the middle bract with apex long-acuminate, margins straight, inner surface white to yellow to pink and glabrous, outer surface red to rose-red and glabrous to puberulous, 12–28 cm long, 6–8 cm wide at base, l/w = 2.9. Floral bracts translucent, persistent, inconspicuous, white to yellow, soft, puberulous abaxially, 4.5–6 cm long, 1.5–2.5 cm wide at base. Flowers 10 to 20 per cincinnus; pedicel pale yellow, puberulous to tomentose, 7–13 mm long; perianth yellow, glabrous to puberulous, 4.6–5.5 cm long, 1–1.2 cm wide at base, at anthesis curved 50–70° and sigmoid; free sepal reflexed, fused sepals with apices not reflexed; staminode white, 1–1.3 cm by 2–3 mm, apex bidentate; stamens with anthers flared outside perianth apex; pollen *trichocarpa* type, medium size (53 × 78 μm), euoblate (P/E = 0.68), isopolar (DR/PR = 1.07), with the distal hemisphere planar, minutely spinulose to verrucose, the proximal hemisphere convex, minutely spinulose to granulose, the germination



MAP 2. Costa Rica and Panama, showing distribution of *Heliconia colgantea* (triangles) and *H. trichocarpa* (circles).

aperture indistinct; ovary white to pale yellow, puberulous to tomentose, 5–8 by 6–9 mm. Drupes tomentose.

SPECIMENS EXAMINED. **Costa Rica.** ALAJUELA: entre Cataratas y La Balsa de San Ramón, elev. 700–800 m, *Brenes 4429* (CR, F), elev. ca. 1000 m, *Kennedy 1657* (MO), elev. ca. 800 m, *Kress et al. 76-605* (DUKE), elev. 2700 ft, *Kress et al. 77-767* (DUKE), *77-807* (DUKE), elev. 900–1000 m, *Stevens 13791* (MO); Finca Los Ensayos ca. 11 mi NW of Zarcero, elev. 850 m, *Croat 43597* (MO); Buena Vista de San Carlos, Quebrada Lajas, Finca Los Ensayos, elev. 850 m, *Jiménez 2323* (CR, F, NY); between San Lorenzo and Los Angeles de San Ramón, above Río San Lorenzo, elev. 620 m, *Burger & Antonio 11190* (F); Colonia Virgen del Socorro, barranca of Río Sarapiquí, elev. 700–800 m, *Stevens 13565* (MO). CARTAGO: forêts de Tuis, elev. 650 m, *Tónduz 11383* (CR, US); woods above Río Pejibaye, 2 km SW of Taus, elev. 740 m, *Lent 2986* (F); near Moravia, elev. 1150–1200 m, *Maas 1075* (U). CARTAGO/LIMÓN: between Turrialba and Siquirres, elev. 2000–2500 ft, *Kress et al. 77-787* (DUKE). GUANACASTE: below Volcán Tenorio along road to Upala, elev. 700 ft, *Kress et al. 80-1217* (DUKE). HEREDIA: Finca La Selva near Puerto Viejo de Sarapiquí, elev. ca. 150 m, *Kress 79-1109* (DUKE). LIMÓN: along Hwy. 32 from Turrialba to Limón, 11 mi S of Siquirres, elev. 650 m, *Croat 43350* (MO). PUNTARENAS: 3.5 mi beyond Golfito in primary forest, elev. ca. 25 m, *Kress et al. 76-592* (DUKE); San Vito de Java, cult. at Los Cruces Trop. Bot. Garden, elev. ca. 4000 ft, *Kress 76-572* (DUKE), *78-975* (DUKE). SAN JOSÉ: streamsides along Río Claro Valley (Río La Hondura drainage), below La Palma, NE of San Jerónimo, elev. 1000–1200 m, *Burger & Burger 7657B* (F). **Panama.** CHIRIQUÍ: Fortuna, elev. 1000–1200 m, *Correa et al. 2668* (MO); upriver from main camp, Fortuna Dam Site, 1200–1400 m, *Folsom et al. 5509* (MO); *Kress & Hammel 83-1605* (DUKE). COCLÉ: El Copé, beyond sawmill, elev. 2800 ft, *Kress et al. 80-1171* (DUKE), *Kress & Hammel 82-1323* (DUKE); El Potroso, elev. 800–1000 m, *Andersson & Sytsma 1276* (S), *D'Arcy 11273* (MO). VERAGUAS: valley of Río Dos Bocas on road between Alto Piedra (above Santa Fé) and Calovébora, elev. 350–400 m, *Croat 27429* (MO), elev. 500 m, *Andersson & Sytsma 1286* (GB, S); beyond Santa Fé above Escuela Agrícola, elev. 2600 ft, *Kress & Cooper-Smith 76-657* (DUKE), *Kress et al. 77-832* (DUKE); Atlantic slope beyond Santa Fé on road to Calovébora, elev. 1200

ft, *Kress et al. 80-1196* (DUKE); Río Calabacito, Aguabal, elev. 400 m, *Maas & Dressler 1624* (MO, U).

PHENOLOGY. Flowering mainly during late rainy season (July to November), peaking September and October.

HABITAT AND DISTRIBUTION. *Heliconia trichocarpa* is distributed throughout Costa Rica and Panama, primarily on the Atlantic slopes at elevations between 100 and 1000 m (MAP 2). This species is found in a wide range of habitats, from stream margins in primary forest understory to roadside embankments in early secondary growth.

VARIATION. Daniels and Stiles (1979) recognized two varieties of *Heliconia trichocarpa*: var. *trichocarpa* and var. *caducispatha*. They listed several characters by which the two taxa differ, the most important one being the rapid postanthesis disintegration of the cincinnal bracts in the latter variety. Although there are some morphological differences, the extent of variation between varieties is not greater than that between populations of var. *trichocarpa* on the Atlantic slopes. In addition, intermediate forms between varieties are known (e.g., *Kress et al. 76-592*, DUKE). For these reasons var. *caducispatha* is not accepted here.

RELATIONSHIPS. *Heliconia trichocarpa* is allied to other species of the *trichocarpa* group with horizontally oriented oblanceolate leaf blades that are widest toward the apex, smaller pendent inflorescences with long-acuminate cincinnal bracts (l/w > 2.5), pubescent ovaries, and pollen with indistinct germination apertures. Its closest relative is *H. colgantea*, from which it differs in its glabrous, red cincinnal bracts, its inconspicuous, decomposing floral bracts, and its glabrous perianth.

6. **Heliconia marginata** (Griggs) Pittier, Man. Pl. Usual. Venez. 299. 1926.
PLATE III, A, B.

Bihai marginata Griggs, Bull. Torrey Bot. Club **42:** 323. 1915. TYPE: Panama, [Darién,] Marraganti and vic., *Williams 696* (holotype, NY!; isotype, US!).

Herb with *Musa*-like habit, 2–3 m tall. Leafy shoots in groups of 20 to over 50; pseudostem gray-green, glabrous, 45–120 cm tall, 4.3–7 cm in diameter; leaves 4 or 5 per shoot, held stiffly erect; petiole green, glabrous, 45–90 cm long, 8–12 mm in diameter; blade with the base unequal, obtuse to attenuate, the apex acuminate, the upper surface green to bright green, glabrous, with midrib green and glabrous, the lower surface green, glabrous to slightly glaucous, with midrib green and glabrous, the longest blade 60–120 by 17–25 cm. Inflorescence pendent, to 40 cm long; peduncle red and green, scurfy, 35–60 cm long, 9–10 mm in diameter; rachis flexuose, red, puberulous to scurfy, 6–12 mm in diameter at base; cincinnal bracts distichous to spirally arranged, 9 to 14 per inflorescence, oriented 90–120° to axis of inflorescence, the basal bract often sterile, the middle bract with apex acute to acuminate, margins straight becoming involute at base, inner surface yellow and glabrous, outer surface red becoming yellow along margins and puberulous, 7–9.5 cm long, 4.5–5.5 cm

wide at base, l/w = 1.7. Floral bracts opaque, persistent, yellow and pink, puberulous to villous abaxially, 5–6 cm long, 1.9–2 cm wide at base. Flowers 7 to 15 per cincinnus; pedicel pale yellow with pink striations, puberulous, 1–1.3 cm long; perianth yellow, glabrous, puberulous along margins, 4.9–5.4 cm long, 8–10 mm wide at base, at anthesis curved 35–45°; free sepal strongly reflexed, fused sepals with apices not reflexed; staminode white, 6–8 by 3–4 mm, apex apiculate, base constricted; stamens with anthers connivent inside apex of corolla tube or slightly flared outside perianth apex; pollen *nutans* type, medium size (51 × 72 μm), euoblate (P/E = 0.71), subisopolar (DR/PR = 2.56), with the distal hemisphere convex, spinulose, the proximal hemisphere planar to subconvex, psilate to granulose, the germination aperture distinctly protruding; ovary pale yellow, glabrous, 9–10 by 5–6 mm. Drupes glabrous, 1.6–1.9 by 1–1.3 cm.

SPECIMENS EXAMINED. **Costa Rica.** PUNTARENAS: 8 mi from Quepos on road to Parrita, ca. sea level, *Kress et al. 77-804* (DUKE); Finca 44 near Río Colorado beyond Villa Neily, elev. ca. 50 ft, *Kress & Cooper-Smith 76-661* (DUKE), *Kress & Clarkson 79-1095* (DUKE); near Coto 47 in herbaceous swamp, sea level, *Maas & McAlpin 1465* (CR, U). **Panama.** DARIÉN: Alconorque swamp on Río Tuira ca. 3 mi NW of El Real, *Duke 4817* (GH, US); .5 mi E of airstrip at El Real, *Lazor & Correa 3398* (SCZ); Cerro Tacarcuna-Serranía, near Yaviza, elev. 50 m, *Gentry & Mori 13506* (MO).

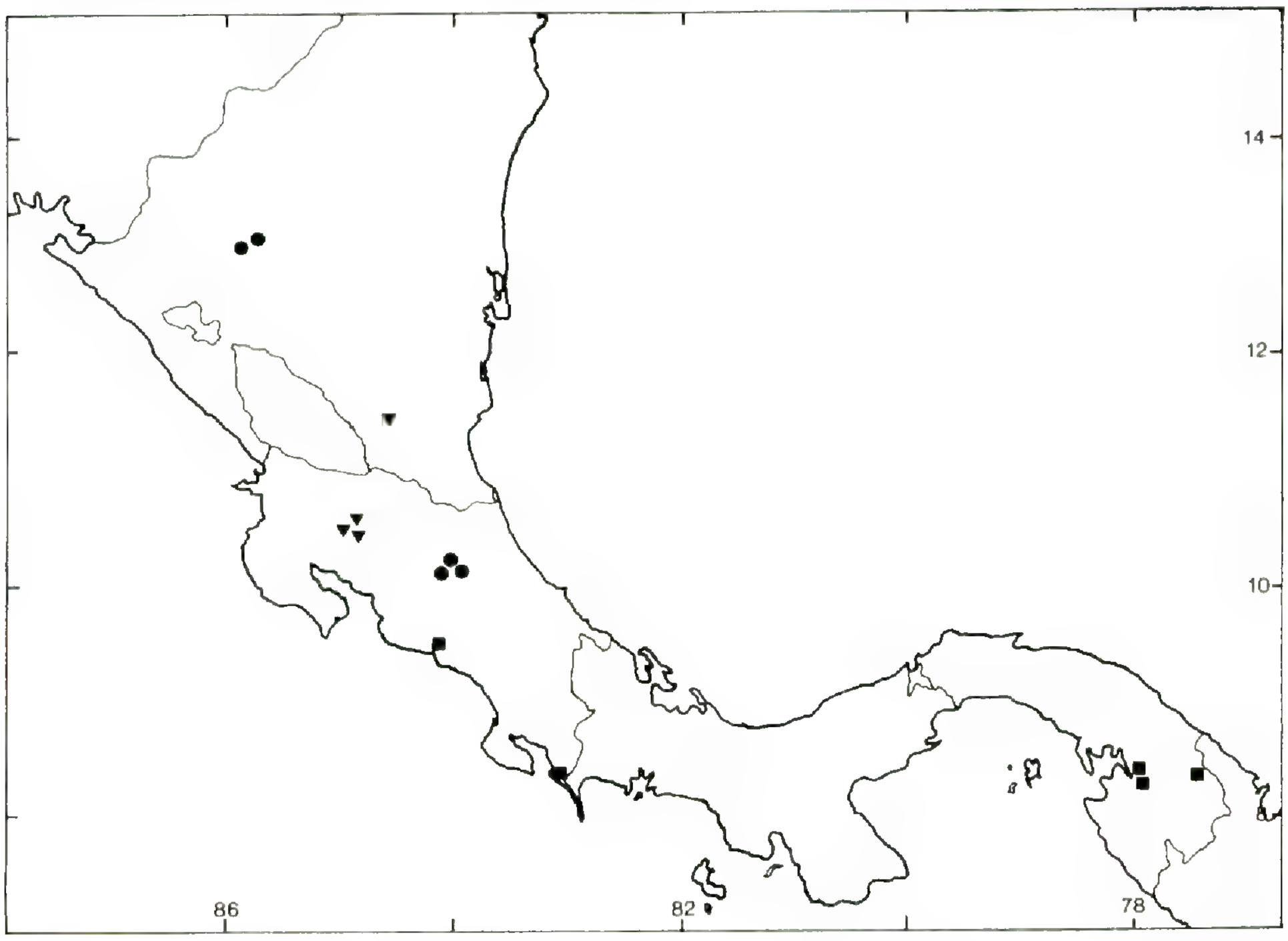
PHENOLOGY. Flowering and fruiting nearly all year, peaking July and August.

HABITAT AND DISTRIBUTION. This species is found on the Pacific Coastal Plain of Costa Rica and Panama, extending north to the Quepos area and south into Darién and South America, where it is more common (see MAP 3). It almost always occurs in dense stands in open swamps or standing water. *Heliconia marginata* is one of the few truly aquatic species of the genus.

RELATIONSHIPS. Among Central American species with pendent inflorescences, *Heliconia marginata* is most closely allied to members of the *nutans* group. However, differences in cincinnal bract morphology, floral structure, and pollen characteristics suggest that this species probably has closer relatives among South American taxa. The small inflorescences with red and yellow cincinnal bracts, the aquatic habitat, and the stiff, erect leaf blades readily distinguish *H. marginata* from other Central American heliconias.

7. **Heliconia secunda** R. R. Smith, Phytologia **30:** 214. 1975. TYPE: Costa Rica, Heredia, along steep slope near road and waterfall, ca. 7 km N of Vara Blanca de Sarapiquí, elev. 5000 ft, *R. R. Smith 2206* (holotype, FLAS; isotypes, A!, GH, MO, US).

Herb with *Musa*-like habit, 2–3 m tall. Leafy shoots solitary or in groups of 2 to 50; pseudostem glabrous, 0.6–2 m tall, 2.5–4 cm in diameter; leaves 2 to 5 per shoot; petiole green, glabrous, 40–120 cm long, 0.8–1.3 cm in diameter; blade with the base unequal, obtuse, the apex acute, the upper surface green, glabrous, with midrib green and glabrous, the lower surface light green to maroon, glabrous, with midrib green to yellow-green and maroon and glabrous to scurfy, the longest blade 80–120 by 20–40 cm. Inflorescence nodding to



MAP 3. Nicaragua, Costa Rica, and Panama, showing distribution of *Heliconia marginata* (squares), *H. secunda* vars. *secunda* (circles) and *viridiflora* (triangles).

pendent (sometimes contorted), to 50 cm long; peduncle red to yellow-red and green, glabrous to scurfy, 3.5–25 cm long, 1–1.3 cm in diameter; rachis flexuose and twisted or contorted, red, glabrous to scurfy, 9–11 mm in diameter at base; cincinnal bracts distichous or spirally arranged, 8 to 12 per inflorescence, oriented 90–120° to axis of inflorescence, the basal bract usually fertile, the middle bract with apex acuminate, margins straight to revolute, inner surface red to orange and glabrous, outer surface red and glabrous to slightly scurfy, 10–14 cm long, 5.3–8 cm wide at base, l/w = 1.8. Floral bracts translucent, slowly decomposing after anthesis, pale yellow, glabrous to puberulous along midrib abaxially, 4–6 cm long, 1.5–2.3 cm wide at base. Flowers 10 to 25 per cincinnus; pedicel white to green to pale yellow, glabrous, 5–10 mm long; perianth yellow to green, glabrous except puberulous along sepal margins, 5–6 cm long, 7–10 mm wide at base, at anthesis curved 20–50°; free sepal reflexed, fused sepals with apices not reflexed; staminode white, apex 7–10 by 3–4 mm, tridentate with center tooth longer than blunt lateral lobes; stamens with anthers flared outside perianth apex; pollen *nutans* type, small (43–44 × 58–62 μm), euoblate (P/E = 0.70–0.74), subisopolar (DR/PR = 2.24–2.55) with the distal hemisphere constricted, convex, spinulose, the proximal hemisphere planar to subconvex, psilate to verrucose, the germination aperture distinctly protruding; ovary light green to yellow, glabrous, 6–9 by 5–6 mm. Drupes glabrous.

DISTRIBUTION. *Heliconia secunda* is found in middle-elevation forests of Costa Rica and Nicaragua (MAP 3).

VARIATION. This species consists of two varieties that differ primarily in flower color.

RELATIONSHIPS. *Heliconia secunda,* a member of the *nutans* group, is closely related to *H. nutans* (with pendent inflorescences) and *H. tortuosa* (with erect inflorescences). It is distinguished from other members of the group by its extremely twisted rachis, which gives the nodding to pendent inflorescences a very contorted appearance.

Key to the Varieties of *Heliconia secunda*

Leaf blade with lower surface green; perianth yellow; ovary pale green. . . . . 7a. var. *secunda.*
Leaf blade with lower surface usually maroon; perianth green; ovary yellow to green. . . . . 7b. var. *viridiflora.*

7a. **Heliconia secunda** var. **secunda** PLATE III, C, D.

Leafy shoots in groups of 10 to 50; pseudostem 1.4–2 m tall, 2.5–4 cm in diameter; leaves 2 or 3 per shoot; petiole 50–100 cm long, 1–1.3 cm in diameter; longest blade 80–120 by 30–40 cm. Inflorescence nodding to pendent, to 50 cm long; peduncle red to yellow-red and green, scurfy, 8–25 cm long, 1–1.3 cm in diameter; rachis scurfy, 9–11 mm in diameter at base; cincinnal bracts spirally arranged, 9 to 12 per inflorescence, oriented 90–120° to axis of inflorescence, the middle bract with margins revolute, inner surface red becoming yellow at midrib, 10–12.5 cm long, 5.3–6 cm wide at base. Floral bracts 4–6 cm long, 1.5–2.3 cm wide at base. Flowers 15 to 25 per cincinnus; pedicel green, 5–10 mm long; perianth yellow, 5.5–6 cm long, 8–10 mm wide at base, at anthesis curved 20–30°; staminode 9–10 by 3 mm; ovary light green, 6–9 by 5–6 mm. Drupes 1.4 by 1 cm.

SPECIMENS EXAMINED. **Nicaragua.** JINOTEGA/MATAGALPA: in forest beside hwy. between Jinotega and Matagalpa, elev. 4000–4500 ft, *Bunting & Licht 981* (F, NY, US). JINOTEGA: region of Las Mercedes, sierra E of Jinotega, chiefly in dense wet mixed virgin forest (cloud forest), elev. 1200–1500 m, *Standley 10724* (F); Hwy. 3, 1.9 km NW of Aranjuez road entrance, elev. 1460–1480 m, *Stevens 9202* (MO). **Costa Rica.** HEREDIA: Catarata El Angel, Río La Paz Grande entre Cariblanco y Vara Blanca, elev. 1350 m, *Jiménez 2048* (F); at waterfall 3 mi from Cinchona, elev. 4100 ft, *Kress & Cooper-Smith 76-529* (DUKE), elev. 4400 ft, *Kress et al. 77-776* (DUKE); vic. of Vara Blanca, elev. 1750–1800 m, *Luteyn 3021* (DUKE); Cinchona, along road to Sarapiquí, near waterfalls, *Sheffy 68* (CR). SAN JOSÉ: Río Claro Valley, below La Palma, NE of San Jerónimo (Río La Hondura drainage), elev. 1000–1200 m, *Burger & Burger 7657A* (F), elev. 1500 m, *Burger & Stolze 5303* (F), *Burger & Visconti 10230* (F); Alto La Palma, elev. 4700 ft, *Kress et al. 77-773* (DUKE); along road between La Palma and La Hondura, *Sheffy 74* (CR); between Cascajal and San Isidro de Coronado, elev. 1600–1700 m, *Taylor 935* (DUKE).

PHENOLOGY. Flowering primarily March to August.

HABITAT AND DISTRIBUTION. *Heliconia secunda* var. *secunda* has been collected only around Jinotega in Nicaragua and in several localities in the Cordillera Central of Costa Rica (MAP 3). This variety inhabits old secondary growth in moist cloud forest at elevations of 1200–1500 m.

7b. **Heliconia secunda** var. **viridiflora** Daniels & Stiles, Brenesia **15**(Supl.): 42. 1979. TYPE: Costa Rica, Alajuela, ca. 2 km N of Bijagua, elev. 350 m, *Stiles s.n.,* 10 Sept. 1977 (holotype, USJ; isotypes, F!, US).

Heliconia viridiflora (Daniels & Stiles) Stiles, Brenesia **18:** 152. 1980.

Leafy shoots solitary or in groups of 2 to 4; pseudostem green, glabrous, 60–150 cm tall, 3–4 cm in diameter; leaves 5 per shoot; petiole 40–120 cm long, 8–10 mm in diameter; blade with base slightly attenuate to obtuse, lower surface green (becoming maroon at higher elevations), longest blade 90–120 by 20–30 cm. Inflorescence nodding or contorted, to 36 cm long; peduncle red, glabrous, 3.5–5 cm long, 1–1.2 cm in diameter; rachis flexuose and contorted, red, glabrous, 1 cm in diameter at base; cincinnal bracts distichous and often all arranged on same side of rachis, 8 to 10 per inflorescence, oriented 90° to axis of inflorescence, the middle bract with margins straight (sometimes overlapping near rachis), inner surface orange becoming red along margins, outer surface glabrous, 11–14 cm long, 7–8 cm wide at base. Floral bracts 4–4.5 cm long, 1.5–2 cm wide at base. Flowers 10 to 15 per cincinnus; pedicel pale yellow, 5–8 mm long; perianth white basally, green distally, 5–5.5 cm long, 7–9 mm wide at base, at anthesis curved 35–50°; staminode 7–10 by 3–4 mm; ovary light green to yellow, 8 by 5–6 mm wide. Fruits not seen.

SPECIMENS EXAMINED. **Nicaragua.** ZELAYA: ca. 6.3 km S of bridge at Colonia Yolaina and ca. 0.8 km S of ridge of Serranía de Yolaina on road to Colonia Manantiales (Colonia Somoza), elev. ca. 200–300 m, *Stevens 4881* (MO). **Costa Rica.** ALAJUELA: 3 km NNE of Bijagua along new road to Upala, elev. 450 m, *Burger & Baker 9815* (F), *9873* (F); wet forest 5 km S of Canalete near Río Zapate, along new road to Upala, elev. 100–200 m, *Burger & Baker 10009* (F). GUANACASTE: below Volcán Tenorio along road to Upala, elev. 800 ft, *Kress et al. 80-1216* (DUKE), elev. ca. 700 ft, *Kress et al. 80-1229* (DUKE). PUNTARENAS: San Vito de Java, cult. at Las Cruces Trop. Bot. Garden, elev. ca. 4000 ft, *Kress 78-1033* (DUKE).

PHENOLOGY. Flowering primarily August to November.

HABITAT AND DISTRIBUTION. *Heliconia secunda* var. *viridiflora* is found in the Cordillera de Yolaina of Nicaragua and the Cordillera de Guanacaste of Costa Rica between 200 and 500 m (MAP 3). This variety inhabits both primary and secondary forests.

RELATIONSHIPS. Variety *viridiflora* differs from the typical variety of *Heliconia secunda* in its flowers with green perianths, and its leaf blades with the lower surfaces varying from green with maroon borders to totally maroon. Because of the nonoverlapping flowering times of the two varieties, Stiles (1980) recognized this taxon as a species distinct from *H. secunda.* This phenological difference is not accepted here as sufficient evidence for elevating var. *viridiflora* to specific rank.

8. **Heliconia nutans** Woodson, Ann. Missouri Bot. Gard. **26:** 276. 1934. TYPE: Panama, Chiriquí, Volcán de Chiriquí, vic. of Casita Alta, *Woodson, Allen, & Seibert 968* (holotype, MO!; isotypes, GH!, MICH, NY!, US!).

FIGURE 10; PLATE III, E, F.

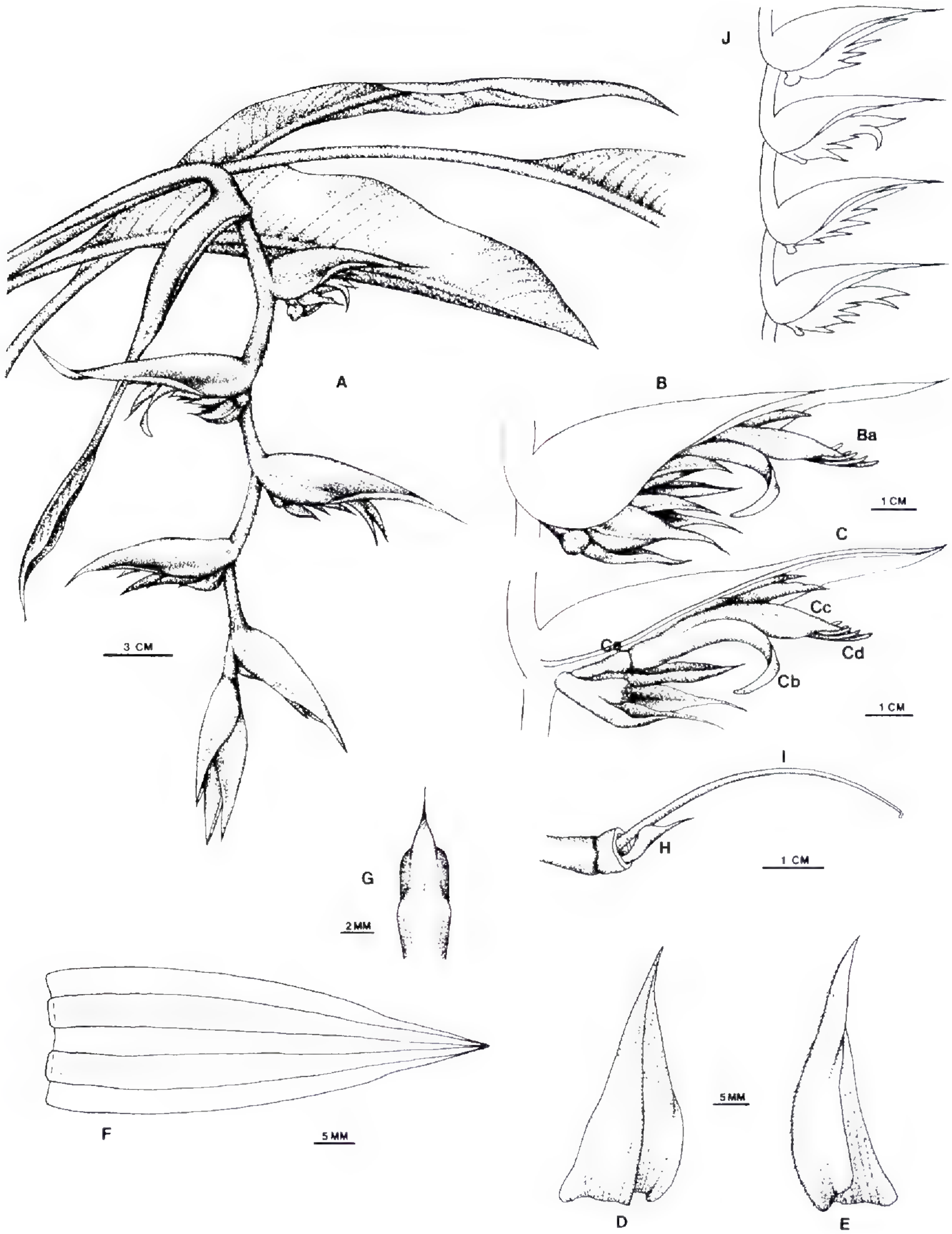


FIGURE 10. *Heliconia nutans*. A, inflorescence. B, C, cincinnal bracts: B, entire (Ba, flower protruding at anthesis); C, cut-away, floral bracts removed showing flower at anthesis (Ca, ovary; Cb, free sepal; Cc, fused sepals, not reflexed; Cd, anthers, exserted). D, E, floral bracts: D, abaxial view; E, lateral view. F, perianth, outer surface showing 2 sepals fused to partially spread-open corolla tube. G, H, staminode: G, abaxial view; H, position relative to style, lateral view. I, style and stigma. J, inflorescence, schematic showing alternative orientation with all cincinnal bracts aligned on 1 side of inflorescence axis.

Heliconia allenii Standley & Williams, Ceiba **3:** 189. 1953. TYPE: Panama, Chiriquí, Río Chiriquí Viejo, vic. Nueva Suiza, elev. 5000 ft, *Allen 6255* (holotype, US!).
Heliconia villosa auct. non Klotzsch: Woodson & Schery, Ann. Missouri Bot. Gard. **32:** 53. 1945, in part (Woodson and Schery included *H. irrasa, H. tortuosa,* and *H. nutans* in *H. villosa*).

Herb with *Musa*-like habit, 1–2.5 m tall. Leafy shoots in groups of 5 to 30; pseudostem light green and maroon, glabrous, 50–160 cm tall, 1.5–3.8 cm in diameter; leaves 3 to 5 per shoot; petiole green and maroon, glabrous, 20–68 cm long, 5–11 mm in diameter; blade with the base unequal, obtuse to truncate, the apex acute, the upper surface dark green, glabrous, with midrib green and glabrous, the lower surface green to maroon, glabrous, with midrib light green to maroon and glabrous to scurfy, the longest blade 50–105 by 15–31 cm. Inflorescence nodding to pendent (sometimes contorted), to 55 cm long; peduncle green and red to solid red; puberulous to tomentose with golden hairs, 5–50 cm long, 5–10 mm in diameter; rachis flexuose (sometimes twisted), red to orange-red (sometimes yellow), puberulous to tomentose with golden hairs, 5–10 mm in diameter at base; cincinnal bracts spirally arranged to distichous (sometimes all bracts aligned on 1 side of inflorescence axis), 5 to 13 per inflorescence, oriented 90–135° to axis of inflorescence, the basal bract often sterile, the middle bract with apex acute to acuminate, margins straight to revolute distally, inner surface red to red-orange and yellow and glabrous to puberulous, outer surface red to red-orange and glabrous to puberulous, 7–11 cm long, 4–7.5 cm wide at base, l/w = 1.6. Floral bracts translucent, persistent and papery when dried or decomposing after anthesis, pale yellow, glabrous to puberulous along midrib abaxially, 3.5–4.5 cm long, 1.3–2 cm wide at base. Flowers 10 to 20 per cincinnus; pedicel white to yellow, glabrous, 4–10 mm long; perianth yellow, glabrous to slightly puberulous, 4–5 cm long, 6–9 mm wide at base, at anthesis curved 30–50°; free sepal straight to reflexed, fused sepals with apices not reflexed; staminode white, apex 7–10 by 3–5 mm, trilobed with rounded lateral lobes; stamens with anthers flared outside perianth apex; pollen *nutans* type, small (46 × 54 μm), suboblate (P/E = 0.87), subisopolar (DR/PR = 2.49) with the distal hemisphere constricted, convex, spinulose, the proximal hemisphere planar to subconvex, psilate to verrucose, the germination pore distinctly protruding; ovary light green, glabrous, 6–7 by 5–6 mm. Drupes glabrous, 1–1.1 by 1–1.1 cm.

SPECIMENS EXAMINED. **Costa Rica.** PUNTARENAS: Las Alturas and vic., elev. 1600–1800 m, *Maas & McAlpin 1486* (NY, U); San Vito de Java, cult. at Las Cruces Trop. Bot. Garden, elev. 4000 ft, *Kress 76-570* (DUKE), *78-901* (DUKE), *78-1024* (DUKE). **Panama.** BOCAS DEL TORO: N slope of Cerro Pate Macho, elev. 1200–1400 m, *Andersson & Sytsma 1311* (S). CHIRIQUÍ: no further locality, *Wagner s.n.,* April 1858 (M); below Cerro Hornito, elev. 1000 m, *Kress et al. 82-1368* (DUKE); Cerro Colorado, along road to copper mine beyond bridge over Río San Félix near town of San Félix, elev. 1390 m, *Croat 37288* (MO); Cerro Colorado, near continental divide, elev. 1500 m, *Antonio 1494* (DUKE, MO), *1531* (DUKE, MO), *1532* (MO), *4859* (DUKE, MO), *4861* (MO), *4863* (MO), *4912* (DUKE, MO); along road between Gualaca and Fortuna Dam site, 10.1 km NW of Los Planes de Hornito, elev. 1260 m, *Antonio 4165* (MO); Gualaca–Fortuna Rd., elev. 1200–1400 m, *Andersson 1306* (GB, S); NO de Campamento Fortuna (Hornito), sitio de regresando al SO del Campamento (Finca Pitti), elev. 1000–1200 m, *Correa et al. s.n.* (MO); La Fortuna

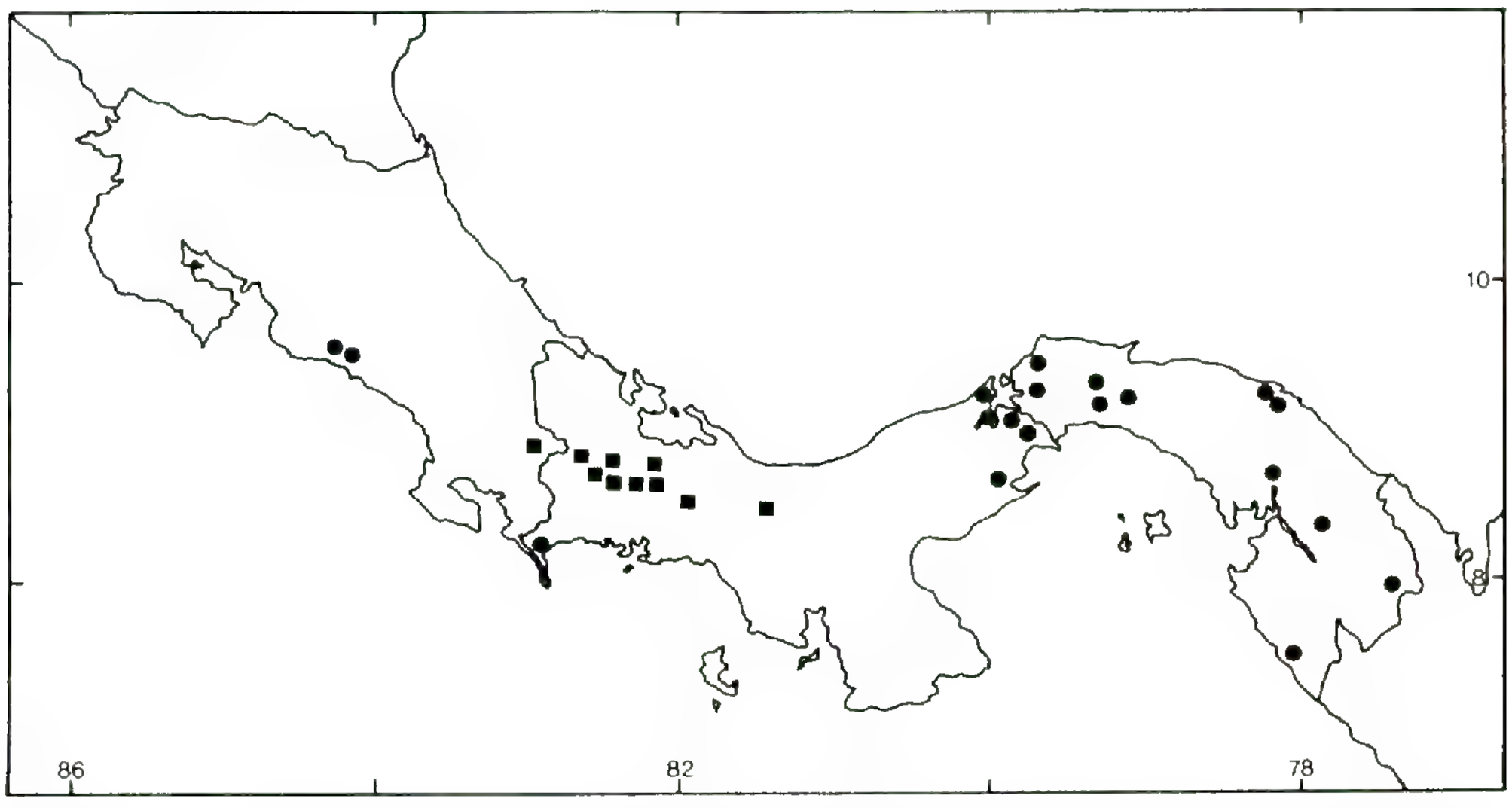
hydroelectric project, elev. ca. 1040 m, *Hammel 1990* (MO); La Fortuna Dam site, elev. 1100 m, *Kress & Hammel 83-1606* (DUKE); *Kress et al. 82-1344* (DUKE), *82-1345* (DUKE), *82-1355* (DUKE), *82-1356* (DUKE); area E of main camp at Fortuna Dam site, elev. 1400–1500 m, *Folsom et al. 5447* (MO); 2 km en el camino Cerro de la Muerte, elev. 6000 ft, *Correa 1244* (PMA); along road 1 km beyond Finca Alto Quiel toward Bajo Mono, elev. 5200 ft, *Luteyn 3716* (DUKE, MO); Cerro Horqueta, TTC-BMI Cloud Forest Litter Study, elev. ca. 1500 m, *Duke et al. 13678* (DUKE, MO, SCZ), *13667* (MO); SW slopes of Cerro Horqueta ca. 6 km NW of Boquete, elev. 1700–1800 m, *Wilbur et al. 15456* (DUKE); NW of Boquete, Cerro Horqueta, elev. 5000–5800 ft, *Dwyer et al. 438* (MO); Cerro Horqueta, elev. 1650 m, *Croat 26994* (MO); vic. of Boquete, lumber road into hills E of Río Caldera, elev. 4500–6500 ft, *Allen 4656* (GH); Boquete, Palo Alto, elev. 1300–1772 m, *Beliz 171* (PMA); Boquete, Finca Collins, *Blum & Dwyer 2583* (MO, SCZ); Monte Rey near Boquete, *Croat 15862* (MO); between Boquete and Monte Rey, *Croat & Porter 15653* (F, MO); E of Boquete on Cerro Azul near Quebrada Jaramillo, elev. 1500–1620 m, *Croat 26791* (MO); Boquete, elev. 3800 ft, *Davidson 668* (F, GH, US); Boquete, 5 mi from town near Finca Lerida, elev. 5300 ft, *Kress et al. 77-822* (DUKE); pastures around El Boquete, elev. 1000–1300 m, *Pittier 2936* (US); Bambito–Cerro Punta, elev. 2100 m, *Cochrane et al. 6294* (MO); Methodist Youth Camp between Nueva Suiza and Cerro Punta, *Croat 26271* (PMA); between Bambito and Cerro Punta, *Croat 10539* (F, MO, NY); Camino entre Bambito y La Amenaza, elev. 6000 ft, *Correa 1281* (PMA); roadside from Cerro Punta to Bambito, *Lazor & Correa 2730* (MO, SCZ); Bambito, elev. 1700 m, *Andersson 1300* (S); lower slope of Baru, E of Bajo Choro region, elev. 6000–6500 ft, *Hammel 3018* (MO); above hwy. along Río Chiriquí between Cerro Punta and Bambito, elev. 5200 ft, *Kress & Clarkson 79-1088* (DUKE); in forest along Río Chiriquí Viejo below Cerro Punta, elev. 5200 ft, *Kress & Clarkson 79-1089a* (DUKE), *79-1089b* (DUKE); Río Chiriquí Viejo, vic. of Nueva Suiza, elev. 5000 ft, *Allen 6255* (US); on road from Río Sereno to Volcán, *Antonio 1304* (MO); 2.2 mi E of El Hato del Volcán, *Luteyn 802* (DUKE); Cerro Pate Macho, elev. 1500–1700 m, *Andersson & Sytsma 1310* (GB, S); Río Chevo, elev. 1650 m, *Knapp 1451* (MO); Cerro Pelota, elev. 2300 m, *Knapp 1499* (MO). VERAGUAS: NE slopes of Cerro Delgadito just NW of Cerro Tute, S of town of Santa Fé, elev. 1000 m, *Luteyn 4039* (DUKE); Cerro Tute, elev. 800–1400 m, *Kress & Knapp 82-1410* (DUKE).

PHENOLOGY. Flowering principally February to August.

HABITAT AND DISTRIBUTION. This species is restricted to altitudes above 1000 m on the Pacific slopes of the western highlands of Panama and neighboring Costa Rica (MAP 4). *Heliconia nutans* inhabits disturbed primary and secondary forests often near streams or rivers. It is the only Central American *Heliconia* with a pendent inflorescence that occurs at elevations over 2000 m.

VARIATION. *Heliconia nutans* is composed of two morphologically distinct entities. One, which occurs primarily around Boquete and Cerro Punta in Chiriquí, Panama, has persistent, papery floral bracts, distichous cincinnal bracts, entirely green leaf blades, and a diminutive stature. The second entity is found in the mountains around La Fortuna and Cerro Colorado in eastern Chiriquí and has decomposing floral bracts, spirally arranged, somewhat contorted cincinnal bracts, maroon or green leaf-blade undersides, and a more robust stature. Their distribution is not entirely allopatric, and where the two entities overlap (e.g., above Gualaca) the first is found at lower elevations and in drier habitats than the second.

RELATIONSHIPS. *Heliconia nutans* is closely related to *H. secunda,* of Costa Rica



MAP 4. Costa Rica and Panama, showing distribution of *Heliconia nutans* (squares) and *H. platystachys* (circles).

and Nicaragua, with which it is often confused in the herbarium. The former species has a puberulous to tomentose rachis, a perianth 4–5 cm in length, and (in some cases) persistent floral bracts that appear papery when dried.

9. **Heliconia platystachys** Baker, Ann. Bot. (London) **7:** 194. 1893 (excl. spec. cit. *Donnell-Smith 1873* (K), which is *H. collinsiana* Griggs var. *velutina* Kress). TYPE: [Colombia,] Santa Marta, *Purdie s.n.* (lectotype, K, chosen by Daniels, Kew Bull. **32:** 682. 1978). PLATE IV, A, C.

Bihai platystachys (Baker) Griggs, Bull. Torrey Bot. Club **31:** 445. 1904.
Heliconia catheta R. R. Smith, Phytologia **30:** 65. 1975. TYPE: Panama, [Panamá,] near old Fort Lorenzo, mouth of Río Chagres, *Piper 6037* (holotype, US!).

Herb with *Musa*-like habit, 3–4 m tall. Leafy shoots in groups of 3 to 20; pseudostem green, glaucous, 1.3–2 m tall, 4–5 cm in diameter; leaves 3 to 6 per shoot; petiole green, glaucous, 90–100 cm long, 1–1.3 cm in diameter; blade with the base unequal, cordate, the apex acute, the upper surface dark green, glabrous, with midrib green and glabrous, the lower surface green, usually glaucous, with midrib light green and glaucous, the longest blade 1.3–1.7 m by 35–40 cm. Inflorescence pendent, to 80 cm long; peduncle red to green, puberulous to tomentose, 10–25 cm long, 1–1.6 cm in diameter; rachis flexuose, red becoming yellow near terminal cincinnal bracts, tomentose, 8–11 mm in diameter at base; cincinnal bracts spirally arranged, 10 to 20 per inflorescence, oriented 90–95° to axis of inflorescence, the basal bract sometimes sterile, the middle bract with apex acuminate, margins straight, inner surface puberulous and yellow-orange becoming green along margins, outer surface puberulous and red basally becoming yellow-green along margins and at apex, 11–16 cm long, 7.5–11 cm wide at base, l/w = 1.5. Floral bracts semitranslucent, decom-

posing after anthesis, yellow, glabrous to minutely puberulous abaxially, 3.5–4.5 cm long, 1–1.5 cm wide at base. Flowers 10 to 15 per cincinnus; pedicel pale yellow, puberulous, 1.5–2.5 cm long; perianth yellow to yellow-green, glabrous to minutely puberulous, 5.5–6 cm long, 1.1–1.3 cm wide at base, at anthesis curved 25–35°; free sepal reflexed, fused sepals with apices slightly reflexed; staminode white, 6–10 by 2–3 mm, apex apiculate; stamens with anthers flared outside perianth apex; pollen *nutans* type, large (62 × 76 μm), suboblate (P/E = 0.82), subisopolar (DR/PR = 2.65), with the distal hemisphere constricted, convex, spinulose, the proximal hemisphere planar to subconvex, psilate to minutely spinulose, the germination aperture distinctly protruding; ovary pale yellow, puberulous to tomentose, 7–10 by 7–8 mm. Drupes sparsely puberulous, 1.7–1.8 by 1.4–1.5 cm.

SPECIMENS EXAMINED. **Costa Rica.** PUNTARENAS: along hwy. 18 km N of Parrita, elev. ca. 25 m, *Kress & Cooper-Smith 76-633* (DUKE); coastal road 11 mi from Parrita, ca. sea level, *Kress et al. 77-803* (DUKE). **Panama.** CANAL ZONE: vic. of Nuevo Emperador, *Blum 2394* (SCZ); near Fort Sherman Military Reservation, *Maas & Mori 1754* (F, U); secondary tropical moist forest along road K-10, 4 km N of Arraiján, elev. 115 m, *Nee 7160* (GH, PMA); near summit of Cerro Pelado, 1 km N of Gamboa, elev. 200–220 m, *Nee 7439* (GH, MO, PMA); Río Agua Salud, near Frijoles, *Piper 5856* (US); Barro Colorado Is., NE of Barrunga Pt. at edge of lake, *Croat 5616* (MO), *5670* (SCZ); near #8 light house clearing, *Croat 6387* (MO), *Dodge 3486* (GH), *Fairchild 17* (F), *Kenozer 232* (US); Summit Garden, *Croat 10790* (F, NY); Albrook Air Force Base Research Forest Site, *Stimson 5068* (DUKE, PMA, SCZ); Albrook, *Dwyer 6599* (MO); along Pipeline Rd. near Gamboa, elev. ca. 75 m, *Kress & Cooper-Smith 76-643* (DUKE), *Kress et al. 77-860* (DUKE); Gaillard Hwy., *Kress 83-1610* (DUKE); Las Cruces Trail, *Croat 11875* (MO). CHIRIQUÍ: Puerto Armuelles, elev. 50 ft, *Davidson 1179* (F); Península de Burica, vic. of San Bartolomé, elev. 0–50 m, *Woodson & Schery 887* (BM), *891* (MO). COLÓN: 18 km past Sardinilla on way to Nombre de Dios, elev. 150–300 m, *Croat 26113* (MO); N of Maria Chiquita on road to Portobelo, *Croat 11353* (MO), *Knapp & Mallet 5718* (MO); between Gatun Lock and Fort Sherman, ca. sea level, *Kress 80-1243* (DUKE); along Hwy. 79, Quebrada Sardinilla, 6 km NE of Buena Vista, elev. 55 m, *Nee 6571* (MO). DARIÉN: Punta Guayabo Grande, along beach, elev. 0–50 m, *Antonio & Hahn 4217* (MO), *Knapp & Mallet 3036* (MO); Santa Fé, elev. ca. 15 m, *Duke 14269* (MO); vic. of Paya, Río Paya, *Stern et al. 427* (GH, MO, UC, US); SW of Jaqué, *Sytsma & D'Arcy 3483* (MO); vic. of Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, *Stern et al. 925* (GH, MO, UC, US). PANAMÁ: Vacamonte Pt., *Allen 2959* (GH, MO); Cerro Campana, elev. 600 m, *Antonio 1260* (MO); vic. of Río Tapia, *Bartlett & Lasser 16623* (MO); TTC Albrook Tower just outside Zone, *Blum 1567* (SCZ); Río Canazas (afluente del Bayano) en el primer campamento, *Carrasquilla & Mendieta 463* (DUKE, PMA); 5 mi from Interamerican Hwy. on road to Cerro Azul, *Croat 11512* (SCZ); near old Fort Lorenzo, mouth of Río Chagres, *Piper 6037* (US); Agricultural Exp. Station at Matias Hernández, *Pittier 6813* (US); near big swamp E of Río Tocumén, *Standley 26726* (US); 5 mi W of Chepo near Interamerican Hwy., *Tyson 6701* (MO, PMA). SAN BLAS: Playón Chico, *Stier 11* (MO), *130* (MO, US). PROVINCE UNKNOWN: *Kuntze s.n.*, Aug. 1874 (NY).

PHENOLOGY. Flowering primarily June to October.

HABITAT AND DISTRIBUTION. This species occurs in undisturbed forest and open secondary growth usually at elevations of less than 100 m, although several collections have been made at 600 m. *Heliconia platystachys* is distributed sporadically along the southern Pacific coast of Costa Rica and into Panama,

where it becomes more abundant in the provinces of Panamá, Colón, and Darién (MAP 4). It is also found in northern South America.

RELATIONSHIPS. In Central America, *Heliconia platystachys,* a member of the *nutans* group, is closely related to *H. collinsiana,* but it has closer relatives in South America. The puberulous cincinnal bracts and ovaries readily distinguish *H. platystachys* from other species of the *nutans* group.

NOMENCLATURE. The confusion over typification of *Heliconia platystachys* has been addressed by Daniels (1978). The problem arose when *H. platystachys* was redescribed by Smith (1975) as *H. catheta* from Panama. Smith made this decision after seeing only part of the type collection of *H. platystachys.* The type housed at Kew consisted of two separate entities: a Colombian collection made by Purdie and a Guatemalan one made by Donnell-Smith. The latter collection, the one seen by Smith, is attributable to *H. collinsiana.* Daniels, based on Baker's protologue, accurately chose the Purdie collection as the lectotype of *H. platystachys,* thereby reducing Smith's *H. catheta* to synonymy.

10. **Heliconia collinsiana** Griggs, Bull. Torrey Bot. Club **30:** 648. 1903. TYPE: Guatemala, Alta Verapaz, near Finca Sepacuité, *Cook & Griggs 352* (US!).

Bihai collinsiana (Griggs) Griggs, Bull. Torrey Bot. Club **31:** 445. 1904.
Heliconia rostrata auct. non Ruiz & Pavon: Standley & Steyerm. Fieldiana Bot. **24:** 184. 1952.

Herb with *Musa*-like habit, 4–6 m tall. Leafy shoots in groups of 3 to 50; pseudostem glabrous to tomentose (sometimes glaucous), 1.2–3 m tall, 3.5–7 cm in diameter; leaves 3 to 5 per shoot; petiole green, glaucous, 40–120 cm long, 1.3–3 cm in diameter; blade with the base unequal, obtuse, the apex acute, the upper surface green to dark green, glabrous, with midrib green and glabrous, the lower surface green, glabrous or with white waxy coating, midrib light green, or maroon and glaucous, the longest blade 1.1–2.5 m by 28–70 cm. Inflorescence pendent, to 72 cm long; peduncle green to red, glabrous to velutinous with rusty hairs, 10–34 cm long, 1.1–1.9 cm in diameter; rachis flexuose, red (sometimes becoming yellow near apex), puberulous to velutinous, 6–13 mm in diameter at base; cincinnal bracts spirally arranged, 7 to 18 per inflorescence, oriented 90–100° to axis of inflorescence, the basal bract sometimes sterile, the middle bract with apex acuminate, margins straight to revolute, inner surface yellow-pink to red and glabrous, outer surface red to orange-red and glabrous to glaucous, 11–17 cm long, 6–8 cm wide at base, l/w = 2.0. Floral bracts opaque and decomposing after anthesis, white to pale yellow, glabrous to puberulous abaxially, 4.5–7 cm long, 1.5–2.5 cm wide at base. Flowers 10 to 20 per cincinnus; pedicel yellow to orange, glabrous to puberulous, 1–3 cm long; perianth yellow to orange, reddish along sepal margins, glabrous to puberulous, 4.6–6 cm long, 8–11 mm wide at base, at anthesis curved 15–25°; free sepal sometimes reflexed, fused sepals with apices not reflexed; staminode white, apex 1–1.7 cm by 3–6 mm, tridentate with center tooth longer than laterals; stamens with anthers flared outside perianth apex;

pollen *nutans* type, small to medium size (52–60 × 52–65 μm), oblate-spheroidal (P/E = 0.92–0.99), subisopolar (DR/PR = 2.67–3.28), with the distal hemisphere convex, spinulose, the proximal hemisphere subconvex, psilate to verrucose, the germination aperture distinctly protruding; ovary yellow to pale green, glabrous, 6–10 by 6–10 mm. Drupes glabrous, 1.2–1.5 by 1.6–1.8 cm.

DISTRIBUTION. This species, found from Mexico to Nicaragua (MAP 5), is composed of two varieties that may overlap in geographic distribution but are separated by elevational differences.

RELATIONSHIPS. *Heliconia collinsiana* and *H. platystachys,* both members of the *nutans* group, are more closely related to each other than to any other Central American members of the genus. However, each of these taxa may be more closely related to some South American species than it is to the other. *Heliconia collinsiana* can be distinguished from *H. platystachys* by its pure red cincinnal bracts and its glabrous floral bracts and ovaries.

REMARKS. Several collections of a taxon that appears to be very closely related to *Heliconia collinsiana* var. *velutina* have been made in the states of Guerrero and Nayarit, Mexico. These plants differ from var. *velutina* in their much smaller stature (ca. 2 m) and their pubescent to tomentose calyxes. Smith (1968) named these individuals *H.* × *mooreana,* believing them to be hybrids of *H. collinsiana* and *H. schiedeana.* Because of the rarity of natural hybrids in *Heliconia* (see section on hybrids) and the multiple collections of this taxon from several different localities in Mexico, Smith's interpretation is not accepted here. However, a decision as to the varietal status of this taxon must await further collections.

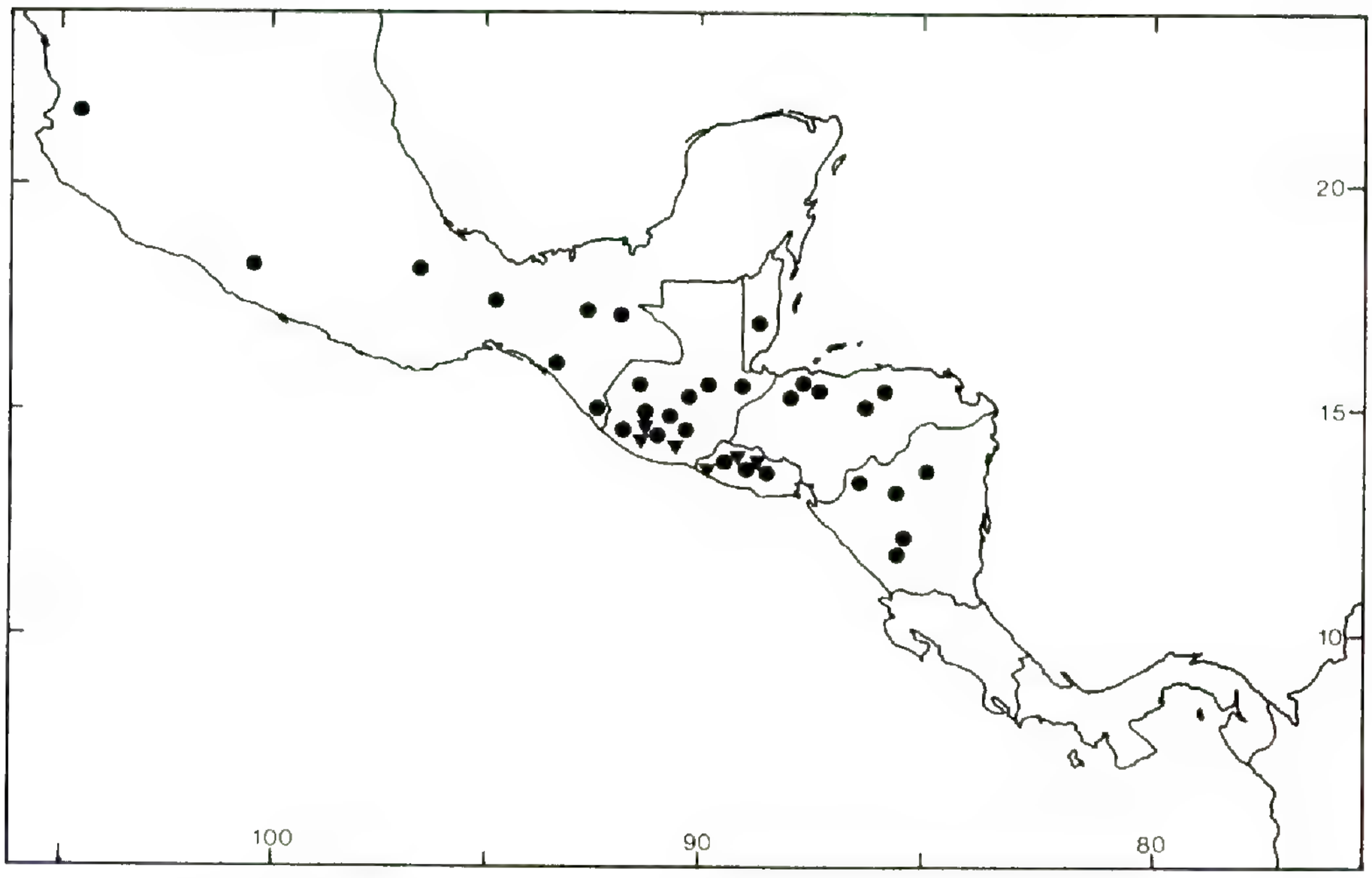
SPECIMENS EXAMINED. **Mexico.** GUERRERO: near km 339 on hwy. to Acapulco below Acahuizatla, elev. 940 m, *Moore 6204* (GH); Acapulco and vic., *Palmer 311* (GH, K, US). NAYARIT: Arroyo de la Cosiscadora, elev. 60 m, *Ortega 49* (US).

Key to the Varieties of *Heliconia collinsiana*

Leaf blades with lower surface glaucous; peduncle and rachis glabrous to tomentose; perianth and ovary yellow. ..... 10a. var. *collinsiana.*
Leaf blades with lower surface not glaucous; peduncle and rachis tomentose to velutinous; perianth orange; ovary green. ..... 10b. var. *velutina.*

10a. **Heliconia collinsiana** Griggs var. **collinsiana** PLATE IV, B, D.

Herb to 4 m tall. Leafy shoots in groups of 5 to 50; pseudostem glaucous, 1.2–1.8 m tall, 3.5–5 cm in diameter; leaves with the petiole light green, 40–62 cm long, 1.3–1.5 cm in diameter, the blade having lower surface green with white waxy coating, the longest blade 1.1–1.5 m by 28–43 cm. Inflorescence with peduncle green to red, glabrous to tomentose, 10–34 cm long, 1.1–1.4 cm in diameter; rachis red, yellow near apical cincinnal bracts, puberulous to tomentose, 6–10 mm in diameter at base; cincinnal bracts 7 to 14 per inflorescence, the basal bract sometimes sterile, the middle bract with margins



MAP 5. Mexico and Central America, showing distribution of *Heliconia collinsiana* vars. *collinsiana* (circles) and *velutina* (triangles).

straight, inner surface yellow-pink to red, outer surface red to orange-red and often glaucous, 11–17 cm long, 6–8 cm wide at base. Floral bracts white to pale yellow, glabrous abaxially, 4.5–7 cm long, 1.5–2 cm wide at base. Flowers 10 to 12 per cincinnus; pedicel yellow to orange-yellow, glabrous to puberulous, 1.3–3 cm long; perianth yellow to orange-yellow, glabrous, 4.6–6 cm long, 8–11 mm wide at base, at anthesis curved 15–25°; staminode 1.1–1.7 cm by 3–6 mm wide; ovary yellow, 6–10 by 6–10 mm.

SPECIMENS EXAMINED. **Mexico.** CHIAPAS: NW side of Cerro Vernal, 25–30 km SE of Tonalá, elev. 400–600 m, *Breedlove 25595* (DUKE, MO); 4 mi N of Tapachula along road to Nuevo Alemán, elev. 250 m, *Croat 43790* (MO); 8.5 mi NE of Escuintla on gravel road to El Triunfo, elev. 250 m, *Croat 43825* (MO); between Esquintla and Monte Ovando, 2.8 km NW of Turquiz, elev. 100 m, *Croat 47469* (MO); Esperanza, Escuintla, *Matuda 16693* (F), *18019* (F); Aguacorte Palenque, *Matuda 3823* (GH); road to microwave tower about 1.7 mi from Hwy. 200, hwy. entrance 5.5 mi NW of Tres Picos, elev. 200 m, *Stevens et al. 2412* (GH); Finca Prusia, municipio de Angel Albino Corzo, elev. 2400 ft, *Ton 3591* (DUKE); N of Huixtla, elev. 500 m, *Taylor 2644* (DUKE). MICHOACÁN/GUERRERO: Sierra Madre, elev. 5–800 m, *Anonymous s.n.*, Jan. 1899 (GH, US). NAYARIT: 8–10 mi W of Tepic along road over mtn. to Jalcocotan, elev. 4000 ft, *Gentry & Gilly 10847* (DUKE). OAXACA: Distr. of Tuxtepec, Chiltepec and vic., elev. 20 m, *Martínez-Calderón 99* (GH, US); ravine 35 km E of Mathias Romero, 4 km W of Palomares on trans-isthmus highway, *Moore 8111* (A). VERACRUZ: Fortin de las Flores (posada Loma), elev. 850 m, cultivado, *Nevling & Gómez-Pompa 312* (GH). **Guatemala.** ALTA VERAPAZ: 22 mi from Tactic near Tucunu, on road to El Estor, elev. 700 ft, *Kress et al. 77-747* (DUKE); vic. of Secanquim, elev. 550 m, *Maxon & Hay 3187* (US); near Pancajche, elev. 360 m, *Standley 70639* (F); Cubilquitz, elev. 350 m, *Von Tuerckheim 8468* (GH, K, NY, US). CHIMALTENANGO: *Johnston 993* (F). CHIQUIMULA: Río Grande (Río Concepción), on Socorro Mtn., above Finca San José, SE of Concepción de las Minas, elev. 1200–1700 m, *Steyermark 31128* (F). ESQUINTLA: between Rodeo and Osuna, below Volcán de Fuego, elev. 2300 ft, *Kress et al. 77-753* (DUKE); La Trinidad on road between Escuintla and Finca

Zapote, elev. 780 m, *Standley 65042* (F); Masagua, elev. 400 m, *J. D. Smith s.n.*, April 1890 (US). HUEHUETENANGO: between Ixcan and Río Ixcan, Sierra de los Cuchumatanes, elev. 150–200 m, *Steyermark 49342* (F). IZABAL: 10–15 km W of El Estor, thickets along road in flat terrain on red clay, *Harmon & Dwyer 4359* (MO, US); vic. of Quirigua, elev. 75–225 m, *Standley 24480* (GH, US). QUEZALTENANGO: El Palmar, elev. 2300 ft, *Kellerman 6078* (F); Palmar, elev. 2300 ft, *Kellerman s.n.*, Feb. 1906 (US). RETALHULEU: Río Talculan W of Retalhuleu, elev. 300 m, *Standley 87338* (F). SAN MARCOS: Río Mopa, below Rodeo, elev. 600 m, *Standley 68796* (F). SANTA ROSA: near El Molino, elev. 600 m, *Standley 78520* (F); region of Platanares, between Taxisco and Guazacapan, elev. 220 m, *Standley 79130* (F). SUCHITEPEQUEZ: Río Sis, elev. 1300 ft, *Donnell-Smith 2804* (K, US); along Río Madre Vieja, above Patulul, elev. 450 m, *Standley 62244* (F); E slopes of Volcán Santa Clara, above Chicacao, elev. 1250 m, *Steyermark 46777* (F); vic. of Tiquisate, elev. 100 m, *Steyermark 47633* (F). **Belize.** STANN CREEK: Middlesex, elev. 200 ft, *Schipp 375* (BM, F, GH, K, MO, NY, UC); Stann Creek R.R., *Gentle 2106* (NY). **El Salvador.** AHUACHAPÁN: along road to Tacuba, 2–3 mi NW of San Francisco Menéndez, elev. 500 m, *Croat 42091* (MO). LA LIBERTAD: Colina de Santa Tecla, *Calderón 1851* (US); Finca Santa María, W of Santa Tecla, elev. 750 m, *Carlson 162* (F), elev. 800 m, *Inst. Trop. Inv. Cient. (ITIC) 1206* (MO). SANTA ANA: elev. 700 m, *ITIC 1201* (MO). SAN SALVADOR: elev. 670 m, *ITIC 1204* (MO); vic. of San Salvador in thicket along stream, elev. 650–850 m, *Standley 20551* (US). SAN VICENTE: vic. of San Vicente, elev. 350–500 m, *Standley 21751* (GH, NY, US). SONSONATE: Finca Chilata, stream bank, *Standley 19330* (GH, NY, US). **Honduras.** ATLÁNTIDA: vic. of San Alejo near Río San Alejo, *Standley 7715* (F); rain forest on slopes, Lancetilla Valley ca. 3 mi S of Tela, elev. 200–500 ft, *Webster et al. 12642* (F, MO); Lancetilla Valley, near Tela, *Pfeifer 2126* (US); E of La Ceiba, in rocky ravine, slopes near Puerte Alto on S.F. Co. R.R., elev. 800 ft, *Yuncker et al. 8537* (F, GH, MO, NY, S, UC, US). COLÓN: Trujillo, Río Negro, *Saunders 556* (NY), *703* (NY). CORTES: Mt. Bella Vista above San Pedro Sula, *Barkley & Leiva s.n.*, 4 Oct. 1969 (GH). OLANCHO: Orillas del Patuca, cerca Río Guayape, *G. Cruz s.n.*, 2 March 1973 (MO); rich soil of montane forest between Cofradia and Rancho Quemado, *Barkley & Errazuri 40307* (MO). **Nicaragua.** GRANADA: Comarca La Fuente, elev. 600 m, *Castro & Montiel 609* (DUKE, MO); Volcán Mombacho, elev. 350–500 m, *Moreno 413* (MO), *439* (MO), *1466* (MO). JINOTEGA: NE de Wiwilí, entre El Carmen y Wamblan, elev. 250–400 m, *Araquistain & Castro 1859* (DUKE), *Araquistain & Moreno 1508* (DUKE). MANAGUA: 2 mi from El Crucero on the Pan Am Hwy., elev. 2700 ft, *Kress et al. 77-758* (DUKE); between El Crucero and house of Finca Santa Julia, elev. 600–900 m, *Standley 8380* (F); along Hwy. 8 ca. 2.4 km SW of intersection with Hwy. 2, km 28, elev. ca. 700 m, *Stevens 3982* (DUKE), *5167* (DUKE). NUEVA SEGOVIA: Jalapa, *Atwood et al. 6773* (MO). ZELAYA: tall forest about Yauya, 18 km SE of La Luz, elev. 150–200 m, *Bunting & Licht 581* (F, NY).

PHENOLOGY. Flowering mainly January to August (dry season and early part of rainy season); some mature inflorescences all year.

HABITAT AND DISTRIBUTION. Variety *collinsiana* inhabits open secondary growth and well-drained soils at middle to higher elevations (up to 1200 m) from southern Mexico to central Nicaragua (MAP 5). It is the northernmost species of *Heliconia* with a pendent inflorescence and is almost completely allopatric with all other species having the same inflorescence type.

10b. **Heliconia collinsiana** Griggs var. **velutina** Kress, J. Arnold Arbor. **69:** 255. 1981. TYPE: Guatemala, Quezaltenango, lower slopes of Volcán Santa María de Jesús, along hwy. to Quezaltenango near Santa María de Jesús, elev. 1450 m, *Kress, Clarkson, & McDade 77-756* (holotype, DUKE; isotypes, F, K).

Herb to 6 m tall. Leafy shoots in groups of 3 to 8; pseudostem glabrous to tomentose, 2.5–3 m tall, 7 cm in diameter; leaves with the petiole green, 1–1.2 m long, 2.5–3 cm in diameter, the blade with lower surface green and glabrous, the longest blade 2.2–2.5 m by 65–70 cm. Inflorescence with peduncle rusty red, velutinous to villous with rusty hairs, 16–30 cm long, 1.5–1.9 cm in diameter; rachis red, tomentose to velutinous, 1.1–1.3 cm in diameter at base; cincinnal bracts 15 to 18 per inflorescence, the basal bract usually fertile, the middle bract with margins revolute, inner surface red, outer surface deep red and glabrous, 14–17 cm long, 6–7.5 cm wide at base. Floral bracts white, glabrous to puberulous abaxially, 5–6 cm long, 1.5–2.5 cm wide at base. Flowers 15 to 20 per cincinnus; pedicel pale orange, puberulous, 1–1.7 cm long; perianth pale orange, glabrous to puberulous, 5.5–5.7 cm long, 8–9 mm wide at base, at anthesis curved 15–20°; staminode 9–12 by 4–5 mm; ovary pale green, 7–8 by 7–9 mm.

SPECIMENS EXAMINED. **Guatemala.** ESCUINTLA: Finca Monterrey, S slope of Volcán de Fuego, elev. 1140–1260 m, *Standley 64533* (F). GUATEMALA: without further locality, elev. 5000 ft, *Donnell-Smith 1873* (K). QUEZALTENANGO: road to Finca Pireneos near Santa María de Jesús, elev. 4000 ft, *Kress et al. 76-663* (DUKE); Volcán Santa María, elev. 4500 ft, *Kellerman 6073* (F), *6076* (US); Finca Pireneos below Santa María de Jesús, elev. 1350–1380 m, *Standley 68427* (F); between Finca Pireneos and Finca Soledad, lower S-facing slopes of Volcán Santa María between Santa María de Jesús and Calahuache, elev. 1300–1400 m, *Steyermark 33575* (F). SANTA ROSA: Cenaguilla, elev. 4000 ft, *Heyde & Lux 4635* (GH, K, US). SUCHITEPEQUEZ: Finca Mocá, in bushy growth at edge of barranca, elev. 5000 ft, *Skutch 2101* (GH). **El Salvador.** AHUACHAPÁN: Sierra de Apaneca in region of Finca Colima, *Standley 20081* (US). SANTA ANA: moist canyon slope, W side of Cerro del Aguila, elev. 1650 m, *Tucker 1291* (F, K, UC, US). SONSONATE: Cerro los Naranjos, *ITIC 1207* (MO).

PHENOLOGY. Flowering and fruiting mainly during dry season (January to April) and early part of rainy period (May to July); some inflorescences produced all year.

HABITAT AND DISTRIBUTION. *Heliconia collinsiana* var. *velutina* is found on steep forested slopes at middle to higher elevations (> 1300 m) in the Guatemalan and Salvadorian highlands (MAP 5). It is one of the few Central American heliconias found at such high elevations.

RELATIONSHIPS. This variety is distinguished from var. *collinsiana* by its greater stature, its lack of glaucous lower leaf surfaces, its hairy peduncle and rachis, its orange flowers, and its growth at higher altitudes (above 1300 m).

11. **Heliconia curtispatha** Petersen *in* Martius & Eichler, Fl. Brasil. **3:** 15. 1890. TYPE: Panama, [Canal Zone,] prope Gatún, M. Jan. Flor., *M. Wagner s.n.*, Jan. 1858 (holotype, M!). PLATE V, A, C.

Bihaia curtispatha (Petersen) Kuntze, Rev. Gen. Pl. **2:** 685. 1891.

Bihai longa Griggs, Bull. Torrey Bot. Club **31:** 446. 1904; *Heliconia longa* (Griggs) Winkler *in* Engler & Prantl, Nat. Pflanzenfam. ed. 2. **15a:** 536. 1930. TYPE: Costa Rica, Alajuela, El Pez road from Buena Vista to San Carlos Valley, *Cook & Collins 47* (holotype, US!).

Heliconia rostrata auct. non Ruiz & Pavon: Woodson & Schery, Ann. Missouri Bot.

Gard. **32:** 54. 1945, in part (Woodson & Schery included *H. curtispatha* and a hybrid in *H. rostrata*).

Herb with *Musa*-like habit, 6–7 m tall. Leafy shoots in groups of 5 to 25; pseudostem green, glabrous, 1.8–3 m tall, 5–6.5 cm in diameter; leaves 4 to 7 per shoot; petiole green to reddish green, glabrous, 90–145 cm long, 1.5–2.3 cm in diameter; blade with the base unequal, cordate, the apex acute, the upper surface dark green, glabrous, with midrib light green to green and glabrous, the lower surface green, covered with white waxy coating, with midrib yellow to red-green and glabrous, the longest blade 1.9–2.3 m by 35–55 cm. Inflorescence pendent, to 1.6 m long; peduncle red (sometimes yellow), glabrous to scurfy, 28–37 cm long, 1.3–1.8 cm in diameter; rachis flexuose, red to red-orange, puberulous to scurfy, 1.2–1.8 cm in diameter at base; cincinnal bracts distichous to spirally arranged, 20 to 40 per inflorescence, oriented 130–145° to axis of inflorescence, the basal bract usually sterile, the middle bract with apex acute to acuminate, margins straight to involute, inner surface yellow-orange to pink and puberulous to tomentose with rusty hairs, outer surface red to yellow-orange near rachis and puberulous, 8.5–11.5 cm long, 6.5–9 cm wide at base, l/w = 1.3. Floral bracts opaque, persistent, white to yellow, tomentose to velutinous abaxially, 5.5–6.5 cm long, 1.6–2.3 cm wide at base. Flowers 10 to 20 per cincinnus; pedicel white to pale yellow, glabrous to puberulous, 1.1–2 cm long; perianth white to yellow and glabrous basally, deep yellow and slightly puberulous toward apex, 5.5–6.5 cm long, 9–10 mm wide at base, at anthesis curved 70–90° and parabolic; free sepal somewhat reflexed, fused sepals with apices reflexed; staminode white, 6–8 by 2–3 mm, apex cuspidate; stamens with anthers connivent inside apex of corolla tube; pollen *curtispatha* type, medium size (57 × 71 μm), suboblate (P/E = 0.82), isopolar (DR/PR = 0.99), with the distal hemisphere subconvex, spinulose, the proximal hemisphere convex, minutely spinulose, the germination pore distinct and somewhat sunken; ovary white, glabrous, 7–11 by 5–7 mm. Drupes glabrous, 1.7 by 1 cm.

SPECIMENS EXAMINED. **Nicaragua.** ZELAYA: 5 mi W of Bonanza, *Atwood & Neill 6995* (MO); 20 mi W of Rama near Río Micito, elev. 200 ft, *Kress et al. 77-759* (DUKE); vic. of El Recreo, on Río Mico, elev. ca. 30 m, *Standley 19407* (F). **Costa Rica.** ALAJUELA: 5 km S of Canalete near Río Zapate and along new road to Upala, elev. 100–200 m, *Burger & Baker 10000* (F); upper Río Sarapiquí near Cariblanco and along road to Colonia Virgen del Socorro, elev. 800 m, *Burger & Antonio 11133* (F); steep bank above Quebrada Arrayanes, Cariblanco, elev. 900 m, *Lent 3536* (F); 8 km NE of Villa Quesada, near Artezalea and Methodist Rural Center, elev. 550 m, *Molina et al. 17219* (F, NY); forests along Río San Rafael, near hot springs, Hacienda La Marina, ca. 14 km NE of Villa Quesada, elev. 50 m, *Molina et al. 17422* (F, NY); near Santa Clara, elev. 2100 ft, *Kress et al. 77-768* (DUKE); near San Miguel, elev. 1700 ft, *Kress & Cooper-Smith 76-531* (DUKE); near San Miguel, *Sheffy 69* (CR). CARTAGO: near Turrialba, 2 km W of Oriente along Río Vueltas, *Sheffy & Tosi 58* (CR). HEREDIA: Finca La Selva, new property, *Hammel 11459* (DUKE). LIMÓN: between Siquirres and Río Pacuare, and hills S of RR bridge over Río Pacuare, elev. 50–100 m, *Burger & Liesner 7000* (F); in old banana plantation 1 km W of Moín, elev. 25 m, *Kress et al. 76-617* (DUKE); 5 mi from Puerto Limón on road to Siquirres, elev. ca. 100 ft, *Kress et al. 77-789* (DUKE); Cimarrones, ca. 10 km E of Siquirres, elev. 200 m, *Maas 1133* (F, U). PUNTARENAS: San Vito de Java, cult. at Las Cruces Trop. Bot. Garden, elev. 4000 ft, *Kress 76-577* (DUKE), *78-1023* (DUKE). SAN JOSÉ: bords du río de las Vueltas, Tucurrique, elev. 635 m, *Tónduz 12923*

(K, M, US, W). PROVINCE UNKNOWN: forêts de Tsallo, elev. 200 m, *Tónduz 9433* (US, W); lieux humides à Zent, elev. 31 m, *Tónduz 14542* (F (photo), NY). **Panama.** CANAL ZONE: Paraiso, *Dwyer 7154* (MO). COCLÉ: between La Junta and Limón, elev. 800–1000 m, 5 hr walk N of Alto Calvario, *Folsom 5882* (MO); above La Pintada on road to Coclecito, elev. 1600–1700 ft, *Kress et al. 80-1165* (DUKE); La Pintada–Cascajal, elev. 700–800 m, *Andersson & Sytsma 1255* (MO, S). COLÓN: forest on hills above road 18 km past Sardinilla on way to Nombre de Dios, elev. 150–300 m, *Croat 26093* (MO); Cerro Santa Rita, elev. 800–900 ft, *Antonio 1787* (MO); Santa Rita Ridge, *Dwyer & Gentry 9549* (F, MO), *Sytsma 1583* (MO); between France Field, Canal Zone, and Cartival, *Standley 30425* (US); along Río Guanche, elev. 40 m, *Antonio 1217* (MO); Río Guanche, elev. 50 ft, *Kress & Hammel 80-1157* (DUKE); Portobelo, Río Buenaventura, at first bridge leaving on road from Portobelo, *Kennedy 468* (PMA); SW of Cerro Bruja, elev. 600–700 m, *Andersson & Sytsma 1241* (G, MO, S). DARIÉN: Punta Guayabo Grande to Río Jaqué, elev. 5–200 m, *Antonio & Hahn 4384* (MO); Enseñada del Guayabo, *Garwood 1200* (MO); between Quebrada Venado and Peje Swamp on headwaters of Río Tuqueza, *Bristan 1041* (MO); E slope of Cerro Sapo, elev. 2500 ft, *Hammel 1319* (MO); Cerro Pirre, *Bristan 517* (NY). PANAMÁ: 3 mi above Goofy Lake near Cerro Azul, *Croat 11571* (F, MO, NY); Cerro Jefe, *D'Arcy et al. 1957* (F, MO), elev. 2300 ft, *Kress et al. 77-864* (DUKE); Alto de Pacora, below Cerro Jefe, elev. 800–900 m, *Kress et al. 76-635* (DUKE), *Kress & Hammel 83-1573* (DUKE); Campo Tres, 3 mi NE of Alto de Pacora, elev. 500–800 m, *Liesner 537* (MO); road to Cartí, *Antonio 1288* (MO); El Llano–Cartí Rd., elev. 100–200 m, *Andersson & Sytsma 1259* (GB, MO, S), elev. 300–400 m, *Folsom 2561* (MO), *Folsom et al. 6190* (MO), *Kress & Hammel 82-1333* (DUKE); 6 km above Pan Am Hwy. on road from El Llano to Cartí-Tupile, elev. ca. 200 m, *Kennedy 1774* (F, MO, NY); 2.4 mi N of Interamerican Hwy. toward El Llano and Cartí, elev. ca. 1700 ft, *Luteyn 4126* (DUKE); El Llano–Cartí Rd., 5 km N of Pan Am Hwy. at El Llano, elev. ca. 300 m, *Nee 7928* (MO, SCZ), premontane wet forest, *Nee 7944* (MO, US). SAN BLAS: hills SW of Puerto Obaldía, *Croat 16721* (MO).

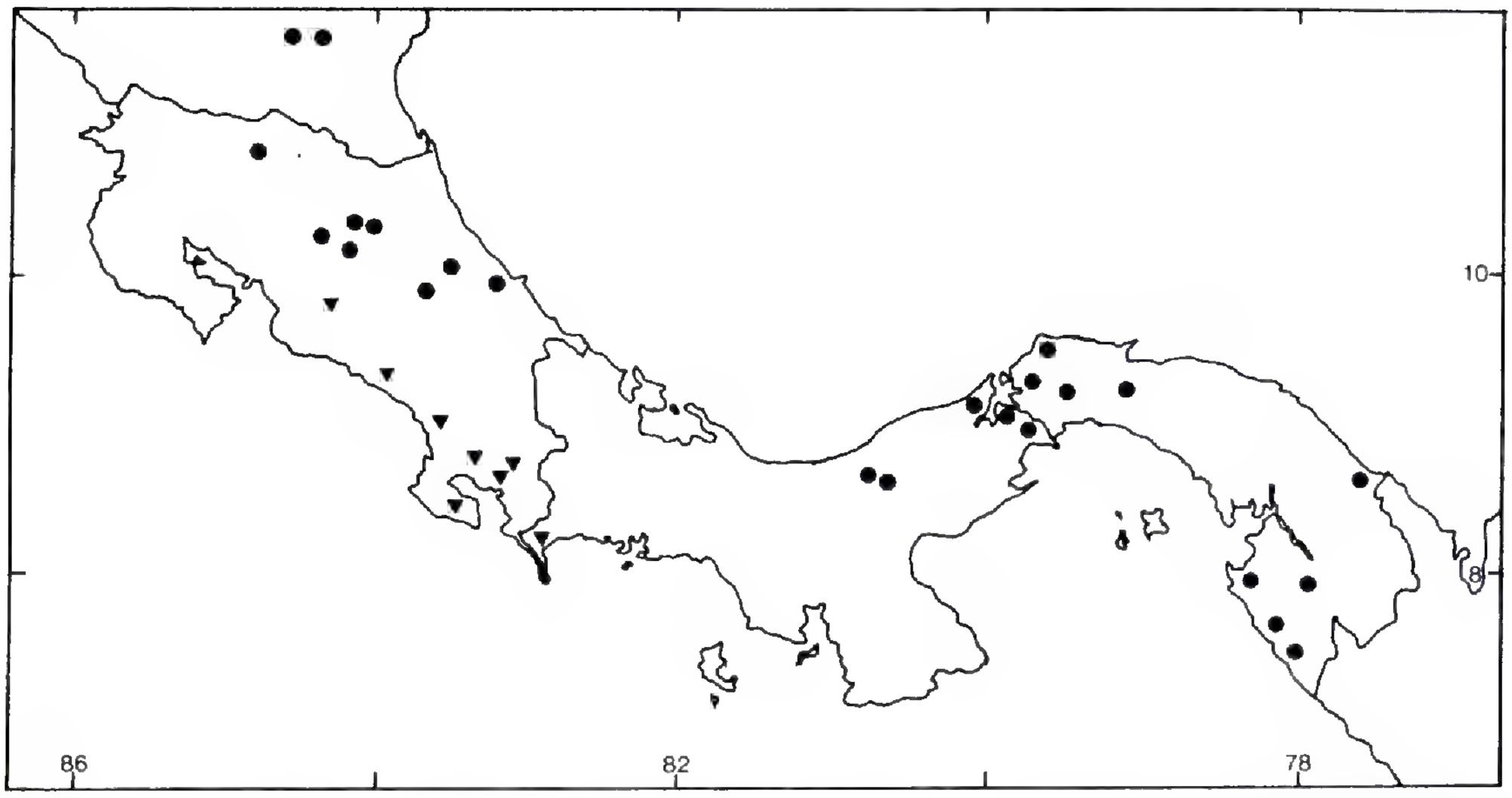
PHENOLOGY. Flowering throughout year, with slight peak during early rainy season (June to September).

HABITAT AND DISTRIBUTION. At higher elevations (above 100 m), *Heliconia curtispatha* inhabits old secondary growth and undisturbed forested slopes. At lower elevations, especially around the Limón area in Costa Rica, this species will invade old banana plantations and other disturbed areas. *Heliconia curtispatha* is distributed from southern Nicaragua to eastern Panama and Colombia. It is primarily found on the Caribbean side of the central cordilleras of Costa Rica and Panama from sea level to 900 m (MAP 6).

VARIATION. *Heliconia curtispatha* is generally morphologically homogeneous except for a distinct color form that is found in the Caribbean lowlands around Limón in Costa Rica. Plants found in this area have distinctive orange to yellow rachises, as opposed to the normal red ones common throughout the range.

RELATIONSHIPS. This species shares a unique common ancestor with *Heliconia stilesii*; together these species constitute the monophyletic *curtispatha* group. This group is allied to the *pogonantha* group but differs in its leaf blades with glaucous lower surfaces and its glabrous, parabolic perianths, as well as in several pollen characters.

NOMENCLATURE. Daniels and Stiles (1979) mistakenly applied Griggs's synonym *Heliconia longa* to this taxon.



MAP 6. Southern Nicaragua, Costa Rica, and Panama, showing allopatric distribution of *Heliconia curtispatha* (circles) and *H. stilesii* (triangles).

12. **Heliconia stilesii** Kress, Brenesia **19/20**: 202. 1982. TYPE: Costa Rica, Puntarenas, slopes above airport at Golfito, elev. 50 ft, *Kress & Clarkson 79-1096* (holotype, DUKE!; isotypes, CR!, F!).

FIGURE 11; PLATE V, B, D.

Heliconia curtispatha auct. non Petersen: Griggs, Bull. Torrey Bot. Club **42:** 316. 1915; Daniels & Stiles, Brenesia **15**(Supl.): 19. 1979.

Heliconia platystachys auct. non Baker: Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **18:** 184. 1937.

Herb with *Musa*-like habit, 5–6 m tall. Leafy shoots in groups of 7 to 16; pseudostem pale yellow-green, glabrous to slightly glaucous, 2.4–3.5 m tall, 6–7 cm in diameter; leaves 4 to 6 per shoot; petiole yellow-green, glabrous, 1.2–1.9 m long, 1.5–2.3 cm in diameter; blade with the base unequal, truncate to cordate, the apex acute, the upper surface dark green, glabrous, midrib light green and glabrous, the lower surface light green, covered with white waxy coating, midrib yellow-green with maroon and glabrous, the longest blade 1.7–2.3 m by 45–55 cm. Inflorescence pendent, to 1 m long; peduncle red, glabrous to scurfy, 10–75 cm long, 1.1–1.8 cm in diameter; rachis strongly flexuose with cincinnal bracts often touching each other, red, scurfy, 1–1.4 cm in diameter at base; cincinnal bracts distichous, 20 to 35 per inflorescence, oriented 135–155° to axis of inflorescence, the basal bract often sterile, the middle bract with apex acute to acuminate, margins straight to overlapping near rachis, inner surface pink to white and pubescent to tomentose with rusty hairs, outer surface rose-red and puberulous to scurfy, 8.5–9 cm long, 6–7.5 cm wide at base, l/w = 1.3. Floral bracts opaque, persistent, pale yellow (sometimes pink), tomentose to velutinous abaxially, 4.5–6.5 cm long, 1.4–1.8 cm wide at base. Flowers 10 to 20 per cincinnus; pedicel white to yellow, glabrous, 1.5–1.9 cm long; perianth white to pale yellow basally, deep yellow toward apex, glabrous, puberulous

along margins, 5.1–6.2 cm long, 1 cm wide at base, at anthesis curved 55–80° and parabolic; free sepal straight to slightly reflexed, fused sepals with apices slightly reflexed; staminode white, 5–8 by 3–4 mm, apex cuspidate; stamens with anthers connivent inside apex of corolla tube; pollen *curtispatha* type, medium size (53 × 66 μm), suboblate (P/E = 0.82), isopolar (DR/PR = 1.17), with the distal hemisphere convex to subconvex, spinulose, the proximal hemisphere convex, minutely spinulose, the germination aperture distinct and somewhat sunken; ovary white, glabrous, 8–9 by 5–6 mm. Drupes glabrous, 1.2–1.5 cm by 7–9 mm.

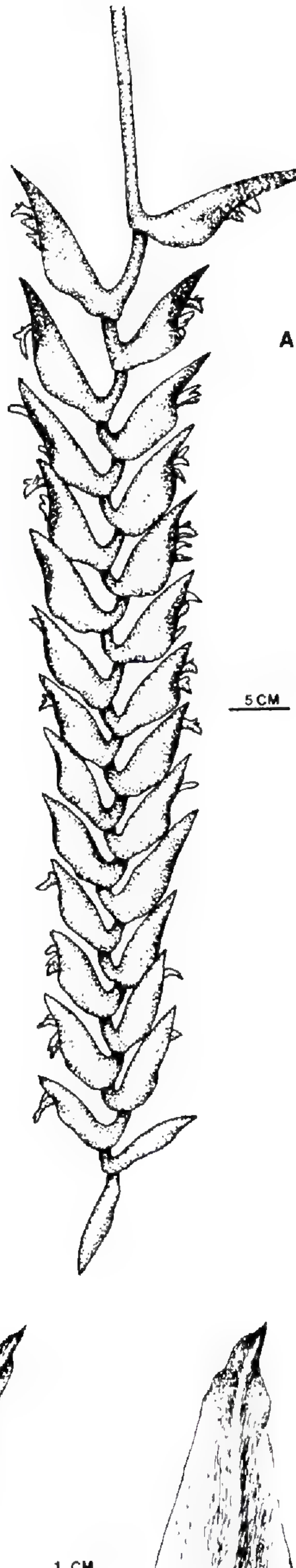
SPECIMENS EXAMINED. **Costa Rica.** PUNTARENAS: 5 km W of Palmar Norte on road to Puerto Cortes, elev. 300 m, *Lent 158* (CR, F); Esquinas Forest, elev. 30 m, *Allen 6289* (GH); entre Los Ríos Piedras Blancas y Esquinas, Osa, elev. 75 m, *Jiménez 2249* (F, NY); Esquinas Forest Reserve near Río Claro, elev. ca. 100 ft, *Kress 78-1047* (DUKE); slopes above Golfito along trail to TV tower, elev. 100–300 m, *Burger & Matta 4769* (F, GH), *4771* (F, US); 12 km E of Golfito, *Harmon & Fuertes 6173* (MO); Golfito, near airport, elev. ca. 50 ft, *Kress 78-1048* (DUKE); 3.5 mi beyond Golfito, ca. sea level, *Kress et al. 76-586* (DUKE); 5 mi above Villa Neily on road to San Vito de Java, elev. 2100 ft, *Kress 78-1050* (DUKE); San Vito de Java, cult. at Las Cruces Trop. Bot. Garden, elev. 3900 ft, *Kress 76-576* (DUKE), *78-1032* (DUKE); Orillas de Mar de Golfito de Osa, *Brenes 12325a* (F); Península de Osa, 5 km W of Rincón de Osa, elev. 50–200 m, *Burger & Gentry 8977* (F), *Burger & Stolze 5469* (CR, F); 4 mi W of Rincón de Osa, near airport, elev. 100 ft, *Raven 21686* (CR, F, NY); Rincón, *Semple 80* (MO), *Sheffy 37* (CR). SAN JOSÉ/PUNTARENAS: between Playa Dominical, Baru, and Tinamastes along road to San Isidro del General, elev. 10–500 m, *Burger & Baker 10138* (F). SAN JOSÉ: along hwy. between Parrita and Santiago near Finca Los Angeles, *Kress & Cooper-Smith 76-634* (DUKE), elev. 2200 ft, *Kress et al. 77-799* (DUKE). **Panama.** CHIRIQUÍ: Península de Burica, 10 mi W of Puerto Armuelles, elev. 100–300 m, *Liesner 85* (F, MO, NY).

PHENOLOGY. Flowering mainly during early part of rainy season (June to September); some inflorescences produced all year.

HABITAT AND DISTRIBUTION. This species is often found on steep slopes in old secondary growth at elevations below 500 m. It is primarily restricted to the drier Pacific slopes and coastal plains of Costa Rica, from the area around Parrita south to the Burica Peninsula (MAP 6).

RELATIONSHIPS. *Heliconia stilesii* is most closely related to *H. curtispatha*, the only other Central American member of the *curtispatha* group. It differs from that species in its extremely flexuose rachis, in its strictly distichous, nearly imbricate cincinnal bracts, and in being mainly restricted to the Pacific slopes of Costa Rica.

FIGURE 11. *Heliconia stilesii*. A, inflorescence. B, C, cincinnal bracts: B, entire (Ba, flower protruding at anthesis); C, cut-away, floral bracts removed showing flower at anthesis (Ca, ovary; Cb, free sepal; Cc, fused sepals, partially reflexed; Cd, anthers, included in apex of corolla tube). D, E, floral bracts: D, abaxial view; E, lateral view. F, perianth, outer surface showing 2 sepals fused to partially spread-open corolla tube. G, H, staminode: G, abaxial view; H, position relative to style, lateral view. I, style and stigma. (© Museo Nacional de Costa Rica, 1982; reprinted with permission.)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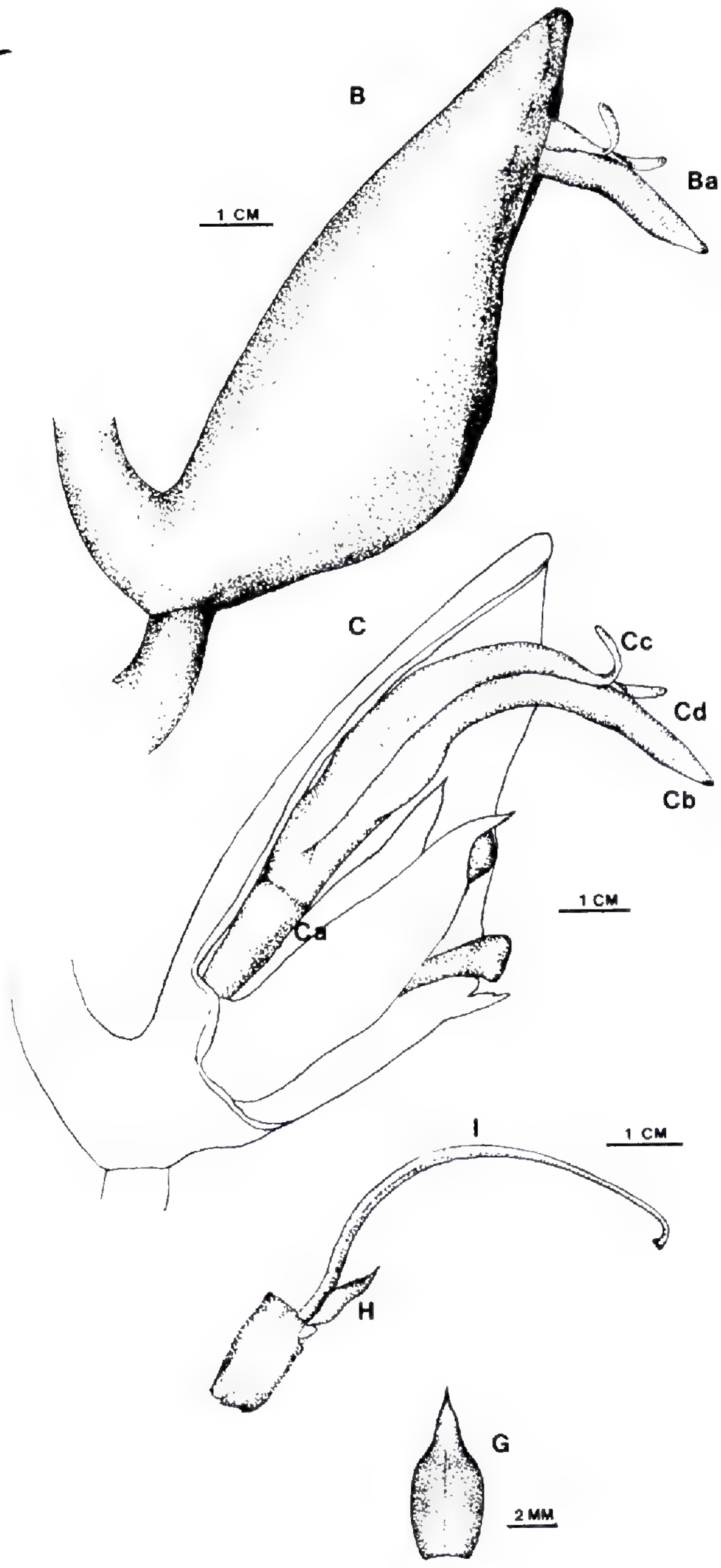
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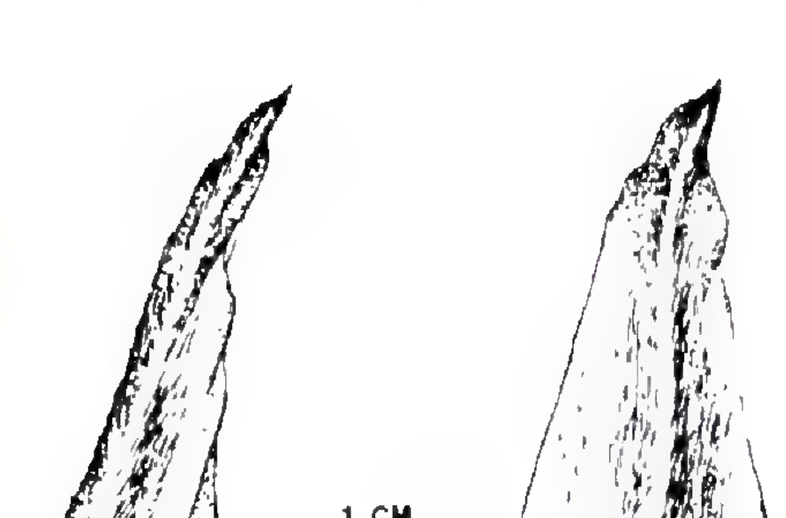
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NOMENCLATURE. Griggs (1915) and later Daniels & Stiles (1979) mistakenly applied the name *Heliconia curtispatha* Peterson to this taxon.

13. **Heliconia sessilis** Kress, J. Arnold Arbor. **62:** 251. 1981. TYPE: Panama, Colón, along road between Gatún Lock and Fort Sherman, elev. ca. 3 m, *Kress 80-1241* (holotype, DUKE!; isotypes, F!, GH!, K! MO!, PMA!).
FIGURE 12; PLATE VI, A, C.

Heliconia pogonantha auct. non Cuf.: Croat, Fl. Barro Colorado Is. 257. 1978.

Herb with *Musa*-like habit, 6–7 m tall. Leafy shoots in groups of 10 to 20; pseudostem green to brown, glabrous, 2.5 m tall, 8–9 cm in diameter; leaves 4 or 5 per shoot; petiole olive green, glabrous, 1.4–1.8 m long, 2 cm in diameter; blade with the base unequal, attenuate to obtuse, the apex acute, the upper surface green, glabrous, with midrib olive green and glabrous, the lower surface dull green, glaucous, with midrib yellow-green with central maroon stripe and slightly glaucous, the longest blade 2 m by 40–60 cm. Inflorescence nodding to pendent, to 90 cm long; peduncle obscure, red, puberulous, 2 cm in diameter; rachis flexuose, red at base of inflorescence, yellow toward distal bracts, puberulous, 1.8–1.9 cm in diameter at base; cincinnal bracts spirally arranged, 23 to 30 per inflorescence, oriented 90° to axis of inflorescence, the basal bract usually sterile, the middle bract with apex acute, margins straight becoming involute near rachis, inner surface white to pink and glabrous to puberulous, the outer surface red and glabrous, 8–9 cm long, 9 cm wide at base, l/w = 0.9. Floral bracts opaque, persistent, pale yellow, pink along margins, puberulous abaxially, 3.5–4 cm long, 1.8–2.1 cm wide at base. Flowers 15 to 20 per cincinnus; pedicel white, reddish near ovary, glabrous, 6–10 mm long; perianth deep yellow distally, paler at base, glabrous except for puberulous sepal margins, 4.8–5.1 cm long, 1.1–1.2 cm wide at base, at anthesis curved 30–40° and slightly sigmoid; free sepal reflexed, fused sepals with apices reflexed; staminode white to pale yellow, 6–7 by 3 mm, apex cuspidate; stamens with anthers connivent inside apex of corolla tube; pollen medium size (57 × 79 μm), euoblate (P/E = 0.72), subisopolar (DR/PR = 2.43), with the distal hemisphere subconvex, spinulose, the proximal hemisphere planar, psilate, the germination aperture distinct, flattened, sunken; ovary white becoming pale lavender around apex, glabrous, 1–1.2 cm by 6–7 mm. No mature fruits seen.

SPECIMENS EXAMINED. **Panama.** CANAL ZONE: vic. of Fort Sherman, W of Colón, near sea level, *Kress & Clarkson 77-871* (DUKE), *Standley 31117* (US); W of Limón Bay, Gatún Locks, and Gatún Lake, *Johnston 1639* (GH); Barro Colorado Is., laboratory clearing, *Croat 12422* (MO, NY, SCZ).

PHENOLOGY. Flowering during wettest part of rainy season (late August probably to December).

HABITAT AND DISTRIBUTION. This species is found in flooded secondary growth in the Atlantic coastal lowlands of Panama (MAP 7). Only a very localized population has been found west of Colón, but this species may be scattered farther east in Panama and even into South America.

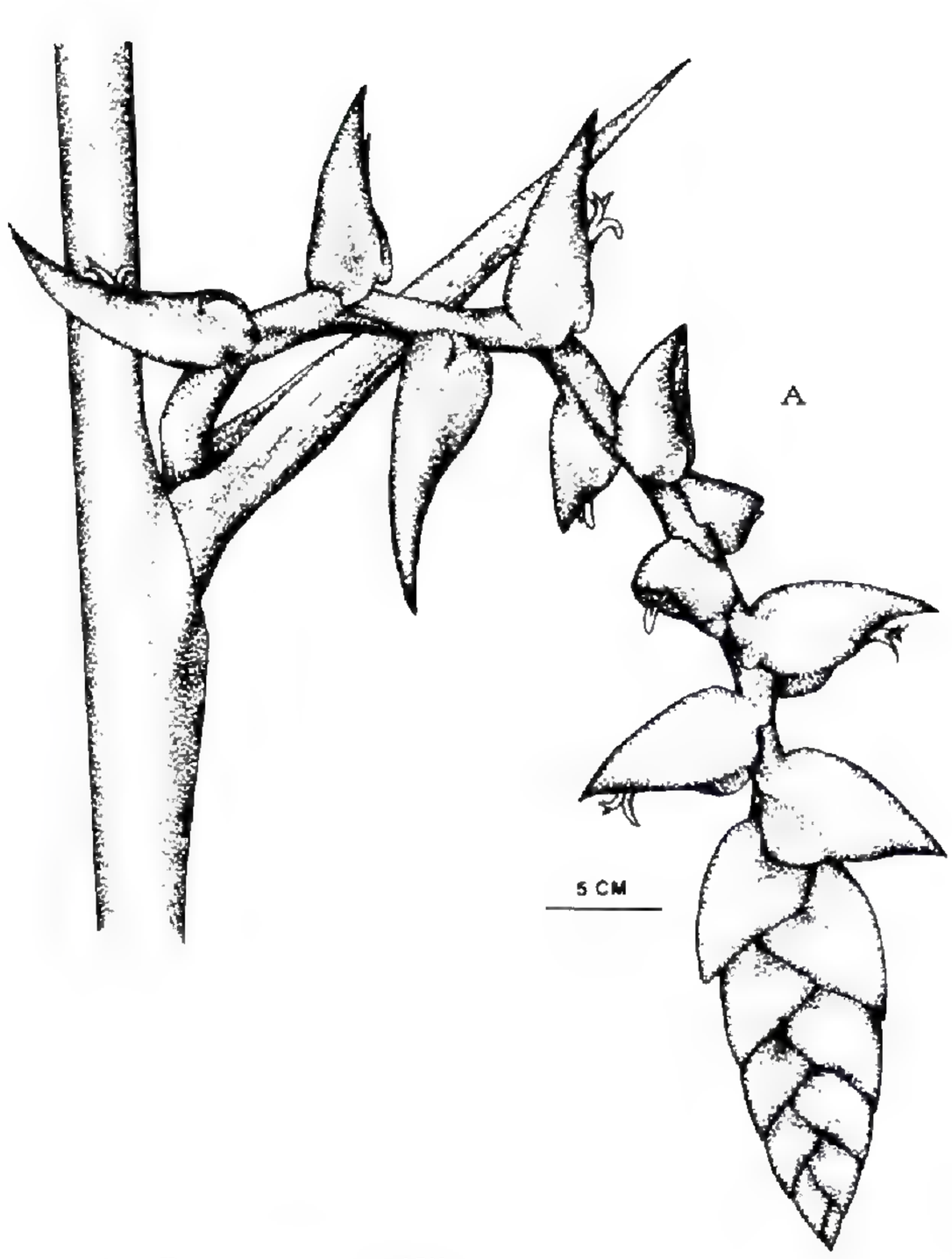
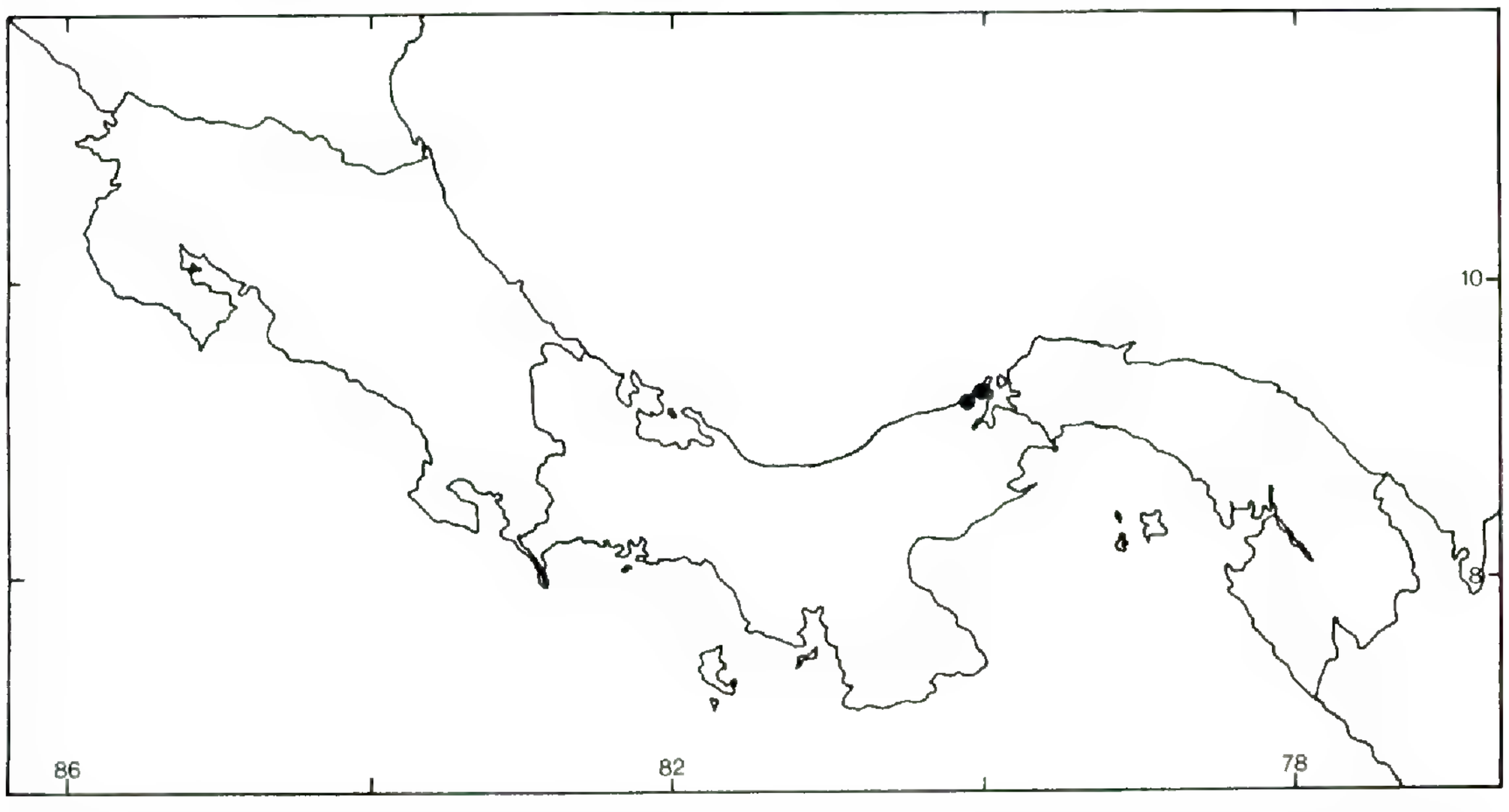


FIGURE 12. *Heliconia sessilis*. A, inflorescence. B, C, cincinnal bracts: B, entire (Ba, flower protruding at anthesis); C, cut-away, floral bracts removed showing flower at anthesis (Ca, ovary; Cb, free sepal; Cc, fused sepals, reflexed; Cd, anthers, included in apex of corolla tube). D, E, floral bracts: D, abaxial view; E, lateral view. F, perianth, outer surface showing 2 sepals fused to partially spread-open corolla tube. G, H, staminode: G, abaxial view; H, position relative to style, lateral view. I, style and stigma.



MAP 7. Costa Rica and Panama, showing restricted distribution of *Heliconia sessilis*.

RELATIONSHIPS. *Heliconia sessilis* is allied to members of the *curtispatha* and *pogonantha* groups with large, leafy shoots and massive inflorescences. However, it most likely belongs to a separate lineage that is made up primarily of taxa found in South America. This species is characterized by its semiaquatic habitat, its attenuate leaf bases, its sessile inflorescences, and its only slightly sigmoid perianths.

14. **Heliconia mariae** J. D. Hooker, J. Proc. Linn. Soc., Bot. **7:** 69. 1864. TYPE: New Granada [Colombia], Bolivar, Betami on the Sinu River (lat. 8° N), *A. Anthoine s.n.*, 1859 (holotype, K!). PLATE VI, B, D.

Bihai mariae (J. D. Hooker) Kuntze, Rev. Gen. Pl. **2:** 684. 1891.

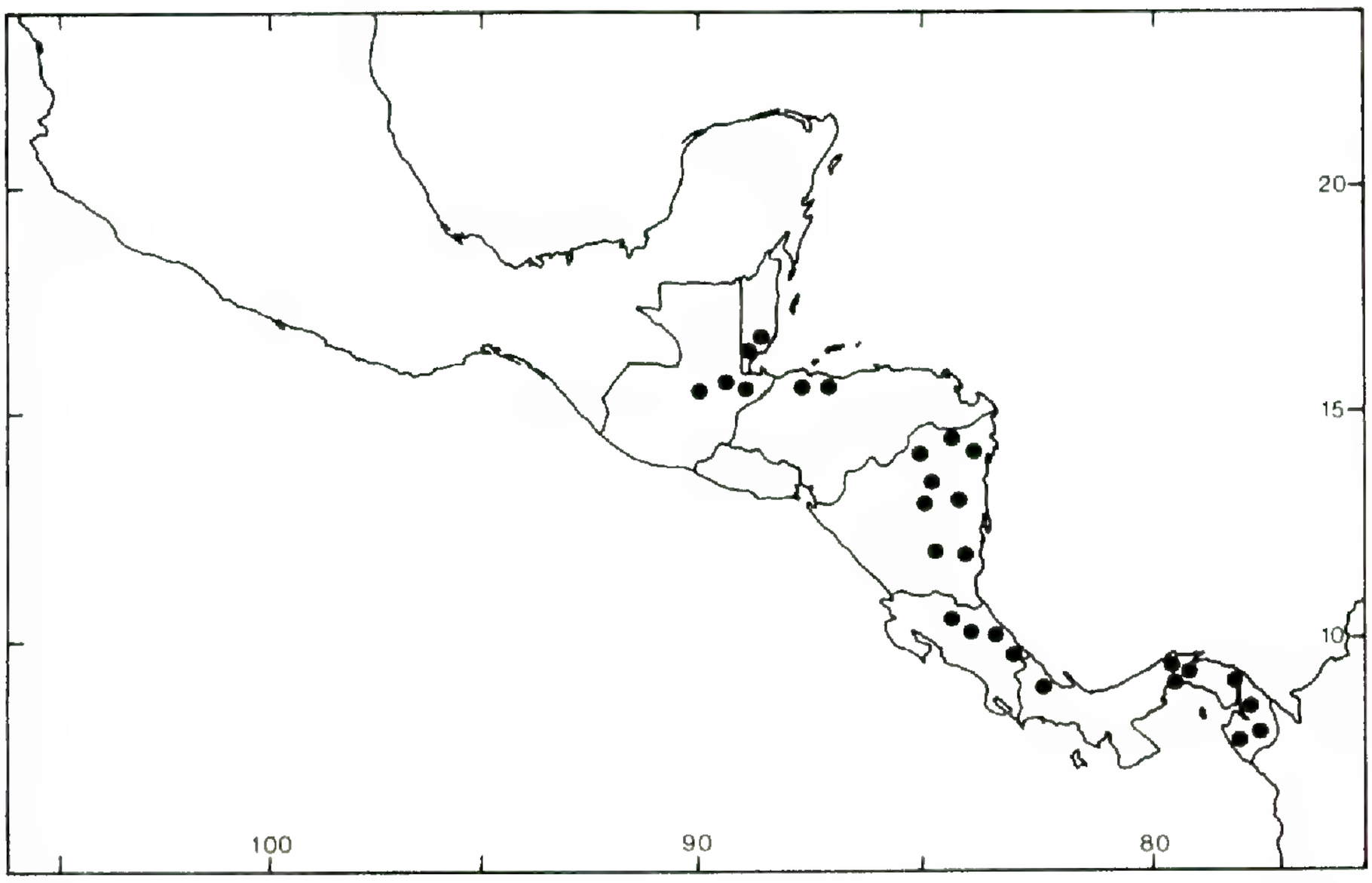
Heliconia elegans Petersen *in* Martius & Eichler, Fl. Brasil. **33:** 12. 1890. *Bihai elegans* (Petersen) Kuntze, Rev. Gen. Pl. **2:** 684. 1891. TYPE: Panama, [Canal Zone,] Paraiso, *M. Wagner s.n.*, Dec. 1857 (holotype, M!).

Bihai punicea Griggs, Bull. Torrey Bot. Club **42:** 321. 1915. *Heliconia punicea* (Griggs) L. B. Smith, Contr. Gray Herb. **124:** 6. 1939. TYPE: Panama, Canal Zone, between Gorgona and Gatún, elev. 10–50 m, *Pittier 2290* (holotype, US!).

Herb with *Musa*-like habit, 4–7.5 m tall. Leafy shoots in groups of 5 to 30; pseudostem red-green, glabrous, 1.9–3.8 m tall, 6–10 cm in diameter; leaves 4 to 6 per shoot; petiole green to yellow-green, often with brown spots, glabrous, 0.9–1.7 m long, 1.5–2.5 cm in diameter; blade with the base unequal, truncate, the apex obtuse to acute, the upper surface green to dark green, glabrous, with midrib light green and glabrous, the lower surface green, glabrous to slightly glaucous, midrib yellow-green with maroon midstripe and glabrous, the longest blade 1.7–2.5 m by 45–65 cm. Inflorescence pendent, long lived, to 65 cm long; peduncle red to yellow-red, densely scurfy, 20–70 cm long, 1.4–1.8 cm in diameter; rachis slightly flexuose, red to yellow, glabrous to scurfy, 1.5–1.8 cm in diameter at base; cincinnal bracts distichous, 40 to 65 per inflorescence, oriented 90–100° to axis of inflorescence, the basal bract usually fertile, the

middle bract with apex acute, margins straight, inner surface white to pink and glabrous, outer surface pink to red (becoming yellowed with age) and glabrous to scurfy, 4.5–6.5 cm long, 7.5–9 cm wide at base, l/w = 0.7. Floral bracts opaque, persistent, white, glabrous to puberulous abaxially, 4–5 cm long, 1.5–2.5 cm wide at base. Flowers 20 to 30 per cincinnus; pedicel white to pink, glabrous to puberulous, 8–15 mm long; perianth white and glabrous basally, pink to red and puberulous apically, 3–4 cm long, 5–6 mm wide at base, at anthesis curved 40–70°, parabolic; free sepal slightly reflexed, fused sepals with apices reflexed; staminode white, 5–7 by 2–3 mm, apex acute to acuminate; stamens with anthers connivent inside perianth apex; pollen *pogonantha* type, medium size (56 × 76 μm), euoblate (P/E = 0.74), heteropolar (DR/PR = 6.84) with the distal hemisphere convex (sometimes truncate), spinulose, the proximal hemisphere planar to subconvex, psilate, the germination aperture distinct, flattened and sunken; ovary white, glabrous, 6–9 by 5–6 mm. Drupes glabrous, 1–1.2 cm by 7–9 mm wide.

SPECIMENS EXAMINED. **Belize.** TOLEDO: Columbia Forest Reserve, ca. 1–2 mi N of entrance, *Croat 24153* (MO); along Aguacate Rd. 0.5 mi from junction with San Antonio road, *Proctor 35858* (MO); Big Fall Estate, Caliente, elev. 20 m, *Whitefoord 1560* (BM). DISTRICT UNKNOWN: Fairview, elev. 200 ft, *Schipp 8413* (F). **Guatemala.** ALTA VERAPAZ: Finca Sepacuite, *Cook & Griggs 787* (US); 28 mi from Tactic on road to El Estor, elev. 650 ft, *Kress et al. 77-745* (DUKE). IZABAL: 6–8 km S of Modesto Mendéz, elev. 110 m, *Harmon 2551* (MO); 70 mi from Flores, just below San Luís de Petén, elev. 1000 ft, *Kress et al. 77-743* (DUKE); jungle bordering Quebrada Roséul, lower slopes bordering E part of Cerro Santa Cruz, NE of San Filipe, elev. 50–150 m, *Steyermark 39638* (F). **Honduras.** ATLÁNTIDA: Lancetilla valley near Tela, N Coast, *Pfeifer 2115* (US); vic. of Tela at sea level, *Standley 53745* (F, US); on slopes near Puente Alto stop on S.F. Co. R.R. E of Ceiba, elev. 900 ft, *Yuncker et al. 8529* (F, GH, NY); Puerto Sierra, near Highland Creek, *Wilson 307* (NY, US). **Nicaragua.** COMARCA DEL CABO: Miguel Bikou, *Robbins 5863a* (MO). JINOTEGA: Salto Acatula, Río Bocay, elev. 130 m, *Stevens et al. 16758* (MO); Valle del Cuá, El Cedro, elev. 700 m, *Moreno 843* (MO), *962* (MO). MATAGALPA: slope of Cerro Musun, Quebrada El Jobo (tributary of Río Paiwas), elev. ca. 300 m, *Stevens 12012* (MO). ZELAYA: Bluefields, Cerro Maypita, 4 km ENE of Rama, elev. ca. 150 m, *Proctor et al. 27357* (F, NY); forest near Yauya, ca. 18 km SE of La Lux, elev. 150–200 m, *Bunting & Licht 579* (F, NY); 40 mi W of Rama, elev. 300 ft, *Kress et al. 77-761* (DUKE); along trail from Cerro Saslaya to San José del Hormiguero, from Loma Mollejones E, halfway to San José del Hormiguero, elev. ca. 200–400 m, *Stevens 7023* (DUKE); vic. of San José del Hormiguero, elev. ca. 120–150 m, *Stevens 7169* (DUKE); about 8–9 km E of Río Kukalaya on road from Puerto Cabezas to Rosita, elev. 200–300 m, *Stevens 8695* (DUKE); Kururia, elev. 50 m, *Pipoly 3984* (MO); Waylawás, elev. 90–200 m, *Pipoly 4197* (MO), *4343* (MO). **Costa Rica.** ALAJUELA: forest near Cerro Negro and along road 18–22 km N of Aguas Zarcas in Llanura de San Carlos, elev. 60 m, *Burger & Stolze 5170* (F); along road between Jabillos and La Fortuna, elev. 600 ft, *Kress et al. 77-771* (DUKE); Llanura de San Carlos, elev. 100 m, *Molina et al. 17657* (F, NY, US). CARTAGO: forêts de Peralta, vallée du Reventazón, elev. 250 m, *Pittier 2360* (K). HEREDIA: Finca La Selva, elev. 100 m, *Kress & Cooper-Smith 76-524* (DUKE); Finca La Selva, W River Road, elev. 100 m, *Kress 79-1104* (DUKE). LIMÓN: along hwy. from Turrialba to Siquirres NE of Chitaria, *Sheffy 36* (CR); near Moín along hwy. to Limón, elev. 25 m, *Kress & Cooper-Smith 76-619* (DUKE); along road between Puerto Viejo and BriBrí, elev. 300 ft, *Kress et al. 77-794* (DUKE); road between BriBrí and Bratsi, along Río Sixaola, elev. 10–50 m, *Burger et al. 10456* (F). PUNTARENAS: Las Cruces Trop. Bot. Garden, cult., elev. 3500 ft, *Kress 78-1022* (DUKE). PROVINCE UNKNOWN: near Platanillo, Toro Amarillo,



MAP 8. Mexico and Central America, showing distribution of *Heliconia mariae*.

Folis 23914 (CR); elev. 31 m, *Tónduz 14551* (CR). **Panama.** BOCAS DEL TORO: vic. of Chiriquí Lagoon, *Von Wedel 2905* (GH, MO). CANAL ZONE: Barro Colorado Is., *Croat 6568* (MO), *Croat 8689* (MO); along K16C, vic. of Cerro Viejo, *Blum 1274* (SCZ); Río Providencia and ridge S of river, elev. 5–170 m, *Nee & Gentry 8714* (MO, PMA); old site of Gorgona, *Maxon 6784* (US); hills near Huile around Gatún Lake, *Smith et al. 3292* (F, US); Empire to Mandingo, *Piper 5437* (US); Cerro Gordo near Culebra, *Standley 26000* (US); hills near Gatún, *Standley 27234* (US); between Gorgona and Gatún, elev. 10–50 m, *Pittier 2290* (US); Pipeline Road, elev. ca. 75 m, *Kress & Cooper-Smith 76-644* (DUKE), *Kress et al. 77-855* (DUKE), *Wilbur & Weaver 11272* (DUKE); along R.R. and Panama Canal, 6 km W of Gamboa, elev. 30–40 m, *Nee 7213* (MO). COLÓN: ridge behind Garotte, *D'Arcy 9323* (US); road between Ft. Sherman and Margarita, elev. 25 ft, *Kress & Clarkson 80-1146* (DUKE); camino hacia San Lorenzo después de Fort Sherman, *Quistgaard 3* (PMA); Río Guanche, elev. 0–50 ft, *Antonio 4821* (MO). DARIÉN: Bayano Dam Bridge, elev. 50 ft, *Antonio 4517* (MO); vic. of Boca de Cupe, elev. ca. 40 m, *Allen 879* (MO); Punta Guayabo Grande, elev. 0–50 m, *Antonio & Hahn 4249* (MO); between Río Jesús and Sabado, elev. ca. 100 ft, *Hammel 1347* (MO); Quebrada Camachi muricate cerca casa de Bartoc, *Kennedy 2831* (MO); tributary Río Correlón, *Sexton 211* (MO). PANAMÁ: Río Espave, *Gentry 3790* (MO, PMA); 3 km S of Alcalde Díaz, elev. 410–440 m, *Nee 8554* (MO). SAN BLAS: Playón Chico and vic. of San Blas, Tappakanti, *Stier 167* (MO); Sasardi, elev. 20 m, *Duke 10119* (NY). PROVINCE UNKNOWN: Tabernilla, *Cowell 272* (NY); Matachin, *Kuntze s.n.*, Aug. 1869 (NY).

PHENOLOGY. Inflorescences very long lived (up to 8 months) from first flowering to fruiting; most plants with inflorescences in various stages all year.

HABITAT AND DISTRIBUTION. This species is found from Belize to Panama and extends into northern South America (MAP 8). It inhabits open secondary growth from sea level to 500 meters on both Atlantic and Pacific coasts, being more abundant on the wetter, Caribbean side. Plants of *Heliconia mariae* are soon shaded out in later successional stages and are almost never found in primary forest habitats.

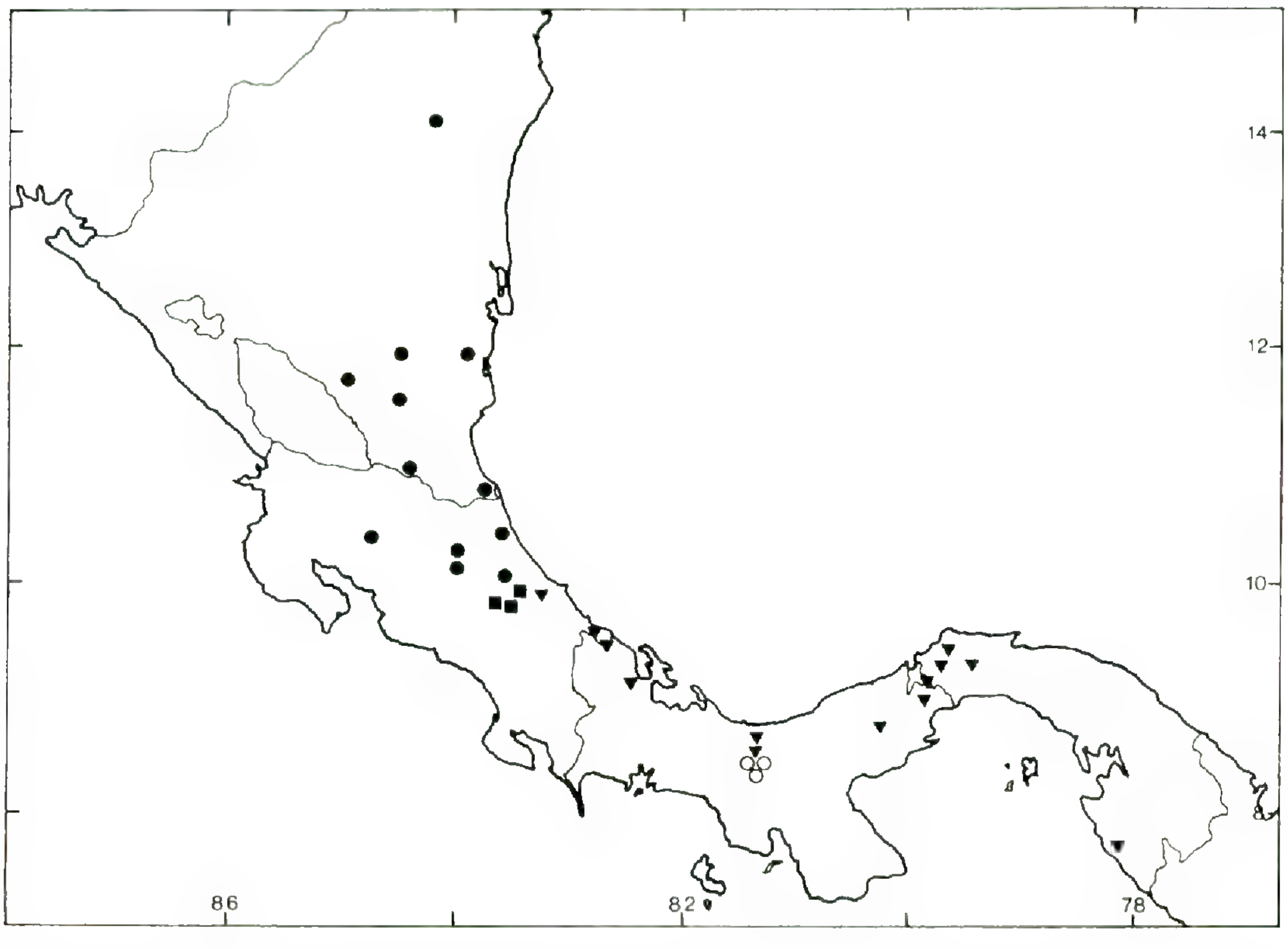
RELATIONSHIPS. *Heliconia mariae* is a member of the *pogonantha* group, but it has several characters derived within that group, including strictly distichous cincinnal bracts, parabolic flowers with red, puberulous perianths less than 4 cm in length, and pollination by territorial nonhermit hummingbirds.

15. **Heliconia pogonantha** Cuf. Arch. Bot. Sist. **9:** 191. 1933. TYPE: Costa Rica, in regione Atlantica, in selva densa ad rivum prope "La Castilla–Los Negritos," 12 km ab ore fluminis Reventazon, *Cufodontis 621* (W) (type destroyed in World War II; Field Museum photograph (Neg. 30912!) remains). NEOTYPE: Costa Rica, Heredia, Puerto Viejo, Finca La Selva, *Daniels & Stiles 14* (F!).

Herb with *Musa*-like habit, 4–7.5 m tall. Leafy shoots in groups of 2 to 20; pseudostem glabrous to scurfy, 1.3–4 m tall, 5–10 cm in diameter; leaves 3 to 6 per shoot; petiole light green to yellow-green, glabrous, 1.1–1.8 m long, 1.5–3 cm in diameter; blade with the base unequal, truncate to cordate, the apex acute, the upper surface dark green, glabrous, with midrib green to yellow-green and glabrous, the lower surface light green to green, slightly glaucous, with midrib yellow-green and maroon and slightly glaucous to scurfy, the longest blade 1.2–3.3 m by 40–65 cm. Inflorescence pendent, to 1.6 m long; peduncle red to yellow, puberulous to woolly, 10–60 cm long, 1.7–2.7 cm in diameter; rachis flexuose, red to yellow, puberulous to velutinous, 1.4–2.5 cm in diameter at base; cincinnal bracts usually spirally arranged, 20 to 55 per inflorescence, oriented 100–145° to axis of inflorescence, the basal bract usually fertile, the middle bract with apex acute to acuminate, margins straight to involute at base, inner surface yellow to red and puberulous to velutinous, outer surface red (sometimes yellow near rachis) and glabrous to velutinous, 8–12.5 cm long, 9–16 cm wide at base, l/w = 0.8. Floral bracts opaque, persistent, white to yellow, tomentose to velutinous with golden hairs abaxially, 5–7 cm long, 1.5–2.5 cm wide at base. Flowers 10 to 30 per cincinnus; pedicel white to yellow to pink, glabrous to puberulous, 7–16 mm long; perianth yellow, glabrous basally, velutinous with golden hairs toward apex, 5–6 cm long, 9–12 mm wide at base, at anthesis curved 45–90° and sigmoid; free sepal slightly reflexed, fused sepals with apices reflexed; staminode white, yellow at apex, 5–9 by 2–3 mm, apex acuminate; stamens with anthers connivent inside apex of corolla tube; pollen *pogonantha* type, large (60–65 × 75–86 μm), euoblate (to sometimes suboblate) (P/E = 0.71–0.84), heteropolar (DR/PR = 6.15–8.08) with the distal hemisphere convex, truncate, spinulose, the proximal hemisphere planar, psilate, the germination aperture distinct, flattened, sunken; ovary white, glabrous, 8–12 by 5–8 mm. Drupes glabrous.

DISTRIBUTION. *Heliconia pogonantha* is widespread in the Neotropics. In Central America (MAP 9) the four geographically distinct varieties generally inhabit moist forested slopes and often invade disturbed open areas from sea level to 1000 m.

VARIATION. The four Central American varieties of *Heliconia pogonantha* differ from each other in inflorescence vestiture and color and in overall size. Additional geographic variants of this species are found in South America.



MAP 9. Nicaragua, Costa Rica, and Panama, showing distribution of *Heliconia pogonantha*: var. *pogonantha* (solid circles), var. *holerythra* (solid triangles), var. *pubescens* (solid squares) and var. *veraguasensis* (open circles).

RELATIONSHIPS. This species is closely related to *Heliconia ramonensis* and other members of the *pogonantha* group. The taxa of this group differ from other heliconias with pendent inflorescences in the usually velutinous to woolly peduncles, rachises, cincinnal bracts, and perianth apices, and in the large pollen grains with flattened, sunken germination apertures. Three of the four Central American varieties of *H. pogonantha* have essentially glabrous inflorescences and are therefore readily distinguished from other members of the *pogonantha* group.

NOMENCLATURE. The neotype of *Heliconia pogonantha* selected by Daniels and Stiles (1979) is in accordance with the protologue provided by Cufodontis. However, the Field Museum photograph of the original type specimen destroyed in World War II is certainly adequate for the correct identification of the species. The necessity for neotypification is therefore questionable.

Key to the Varieties of *Heliconia pogonantha*

A. Inflorescence entirely red. ..... 15b. var. *holerythra*.

A. Inflorescence red and yellow.

B. Peduncle, rachis, and cincinnal bracts velutinous to woolly. ..... 15c. var. *pubescens*.

B. Peduncle, rachis, and cincinnal bracts glabrous to puberulous.

C. Plants less than 5 m in height; lower surface of leaf blade maroon tinted;

cincinnal bracts oriented 115–135° to axis of inflorescence at maturity. . . . . 15d. var. *veraguasensis.*

C. Plants greater than 5 m in height; lower surface of leaf blade green; cincinnal bracts oriented 100–120° to axis of inflorescence at maturity. . . . . 15a. var. *pogonantha.*

15a. **Heliconia pogonantha** var. **pogonantha**

Herb 5–7 m tall. Leafy shoots in groups of 3 to 11; pseudostem bronzy green, glabrous, 2–4 m tall, 6–8 cm in diameter; leaves 4 or 5 per shoot; petiole light green to green, 1.3–1.8 m long, 2–3 cm in diameter; longest blade 2.4–3.3 m by 41–62 cm. Inflorescence to 1.5 m long; peduncle puberulous to scurfy, 25–55 cm long, 1.8–2.7 cm in diameter; rachis yellow, puberulous to scurfy, 1.4–2.5 cm in diameter at base; cincinnal bracts 25 to 55 per inflorescence, oriented 100–120° to axis of inflorescence, the middle bract with margins straight to involute at base, inner surface yellow to pink and velutinous with golden hairs, outer surface red becoming yellow near rachis and puberulous to scurfy, 8–9.5 cm long, 9.5–12 cm wide at base. Floral bracts tomentose to velutinous with golden hairs abaxially, 4–5 cm long, 1.7–2.5 cm wide at base. Flowers 15 to 30 per cincinnus; pedicel pale yellow, glabrous, 9–12 mm long; perianth 5–5.8 cm long, 9–11 mm wide at base, at anthesis curved 45–70°; staminode 7–9 by 2–3 mm; ovary 1–1.1 cm by 6–8 mm.

SPECIMENS EXAMINED. **Nicaragua.** CHONTALES: ca. 4.5 km S of Hwy. 7 on road to Nueva Guinea, elev. ca. 200 m, *Stevens 4949* (DUKE). RÍO SAN JUAN: near Caño Chontaleño, 20 km NE of El Castillo (Río Indio watershed), elev. 200 m, *Neill 3425* (DUKE); in forest along Río San Juan between San Juan del Norte (Greytown) and Delta de San Juan, elev. 0–50 m, *Bunting & Licht 883* (F, NY). ZELAYA: Bluefields, summit and slopes of Cerro San Isidro, elev. 0–65 m, *Proctor et al. 27292* (F, NY); 20 mi W of Rama, elev. 200 ft, *Kress et al. 77-760* (DUKE); along road to Colonia Yolaina, Colonia La Esperanza, ca. 1.3 km SE of intersection with road between Nueva Guinea and Colonia Verdún, elev. 180–200 m, *Stevens 6349* (MO); along road between Río Blanco and Río Copalar, elev. 200–400 m, *Stevens 12100* (DUKE, MO); 8 km E of bridge E of Rosita on road to Bonanza, elev. 90 m, *Stevens 12594* (DUKE, MO); Bonanza, elev. 250–350 m, *Stevens 18793* (MO). **Costa Rica.** GUANACASTE: below Volcán Tenorio, elev. 700 ft, *Kress 80-1218* (DUKE). HEREDIA: Finca La Selva, elev. 100 m, *Burger & Stolze 5785* (CR, F, GH, NY), *Kress 76-523* (DUKE), *79-1102* (DUKE), *Sheffy 53* (CR); near Tirimbina, E of Río Sarapiquí, elev. 150–250 m, *Burger & Burger 8123* (F); near Puerto Viejo along road near Río Sucio, elev. 20 m, *Croat 35722* (MO); La Virgen, along Río San Ramón, elev. 650 ft, *Kress et al. 77-778* (DUKE). LIMÓN: N end of Tortuguero Park, elev. 0–30 m, *Burger & Antonio 11222* (F); La Suerte, W of Tortuguero, elev. 40 m, *Davidson & Donahue 8558* (GB); Finca Montecristo, on Río Reventazón below Cairo, elev. 25 m, *Standley & Valerio 48984* (US). PUNTARENAS: Península de Osa, 5 km W of Rincón de Osa, elev. 50–200 m, *Burger & Gentry 9259* (F); San Vito de Java, cult. at Las Cruces Trop. Bot. Garden, elev. ca. 4000 ft, *Kress 76-569* (DUKE), *Kress 78-1028* (DUKE). PROVINCE UNKNOWN: lieux humides à Lent, elev. 31 m, *Tónduz 14542* (photo, MO).

PHENOLOGY. Flowering primarily during dry and early rainy seasons (January to August); some inflorescences produced nearly all year.

HABITAT AND DISTRIBUTION. *Heliconia pogonantha* var. *pogonantha* is restricted to the wet Atlantic lowlands below 300 m in Nicaragua and Costa Rica

north of Limón (MAP 9). This variety is found in wooded late secondary growth and often develops large stands in light gaps and along forest margins.

15b. **Heliconia pogonantha** var. **holerythra** Daniels & Stiles, Brenesia **15**(Supl.): 39. 1979. TYPE: Costa Rica, Limón, Río Sand Box, 2 km NE of BriBrí, *Baker & Burger 80* (holotype, F!).

Herb 4.5–7.5 m tall. Leafy shoots in groups of 2 to 18; pseudostem 1.4–2.6 m tall, 7–10 cm in diameter; leaves 3 to 6 per shoot; petiole 1.1–1.8 m long, 2–3 cm in diameter; longest blade 2–2.3 m by 40–65 cm. Inflorescence to 1.6 m long; peduncle red, scurfy, 20–60 cm long, 1.7–2.5 cm in diameter; rachis red, scurfy, 2–2.5 cm in diameter at base; cincinnal bracts 30 to 40 per inflorescence, oriented 120–140° to axis of inflorescence, the middle bract with apex acute to acuminate, often necrotic, margins straight (sometimes necrotic), inner surface puberulous, outer surface red and puberulous to scurfy, 10–12.5 cm long, 11–16 cm wide at base. Floral bracts tomentose to velutinous abaxially, 5–7 cm long, 2–2.5 cm wide at base. Flowers 15 to 30 per cincinnus; pedicel white to pink, glabrous, 1.2–1.6 cm long; perianth white to pink basally, yellow at apex, 5–5.7 cm long, 1–1.2 cm wide at base, at anthesis curved 75–85°; staminode 6–8 by 3 mm; ovary white (sometimes slightly maroon), 9–10 by 6–7 mm. Drupes 1.5–2 by 1–1.3 cm.

SPECIMENS EXAMINED. **Costa Rica.** ALAJUELA: 38 km from Interamerican Hwy. toward Upala, *Wilbur 20062* (DUKE). LIMÓN: 5–15 km from Siquirres on new road to Limón, elev. 50–100 m, *Baker & Burger 184* (DUKE, F); Cimarrones, E of Siquirres, elev. 200 m, *Maas 1134* (U); 1–3 km N of BriBrí, Río Sixaola Drainage, elev. 20–200 m, *Burger & Antonio 10981* (F); between Puerto Viejo and BriBrí, elev. ca. 300 ft, *Kress et al. 77-790* (DUKE). **Panama.** BOCAS DEL TORO: top of second fila above Almirante, *Gentry 2813* (F, MO, NY). CANAL ZONE: along Transisthmian Hwy., 10 km from Colón turnoff, elev. ca. 300 ft, *Kress & Clarkson 80-1150* (DUKE); Pipeline Road, *Andersson & Sytsma 1233* (GB, S); along Río Mendosa near Pipeline Road bridge, 8 km NW of Gamboa, elev. 95 m, *Nee 7742* (US). COCLÉ: above La Pintada on road to Coclecito, elev. 1600–1700 ft, *Kress et al. 80-1164* (DUKE). COLÓN: E Santa Rita Ridge lumber road, *Correa & Dressler 619* (SCZ); Santa Rita Hills, *C. E. Smith & H. M. Smith 3447* (F, US); Santa Rita Ridge, *Gentry & Dwyer 9550* (MO); Santa Rita, 4 km desviacíon de la Transístmica, Cuadro 1, elev. 150 m, *Gómez-Pompa et al. 3222* (MO, PMA); near Guasimo along river, *Croat 9954* (MO); Río Guanche, elev. ca. 25 m, *Kress & Cooper-Smith 76-658* (DUKE); Río Buenaventura, 3 mi from Portobelo, ca. sea level, *Kress et al. 77-874* (DUKE); below Cerro Bruja, elev. 600–700 m, *Andersson & Sytsma 1240* (GB, MO, S). DARIÉN: trail from Punta Guayabo Grande to Río Jaqué, elev. 50–200 m, *Antonio & Hahn 4385* (MO). PANAMÁ: Alto de Pacora below Cerro Jefe, elev. 800–900 m, *Kress et al. 76-636* (DUKE); El Llano–Cartí Road, elev. 1600 ft, *Kress & Hammel 82-1334* (DUKE). VERAGUAS: valley of Río Dos Bocas on road between Alto Piedra (above Santa Fé) and Calovébora, elev. 350–400 m, *Croat 27390* (MO); valley of Río Dos Bocas, 11 km from Escuela Agrícola Alto Piedra above Santa Fé on road to Calovébora, elev. 450 m, *Croat 27515* (MO); Atlantic slope, beyond Santa Fé on road to Calovébora, elev. 1200 ft, *Kress et al. 80-1199* (DUKE).

PHENOLOGY. Flowering primarily during dry and early rainy seasons (January to August).

HABITAT AND DISTRIBUTION. This variety is found on the Atlantic slopes and coastal plains of Costa Rica and Panama from Limón to Darién, extending

into South America (MAP 9). It is most common at elevations from sea level to 200 m but occurs to over 800 m. Variety *holerythra* prefers open disturbed habitats, often near streams or rivers.

RELATIONSHIPS. Variety *holerythra* differs from other varieties of *Heliconia pogonantha* in its greater overall stature, its puberulous to scurfy, entirely red inflorescences, and its large, heavy cincinnal bracts.

15c. **Heliconia pogonantha** var. **pubescens** Daniels & Stiles, Brenesia **15**(Supl.): 37. 1979. TYPE: Costa Rica, [Limón,] Turrialba–Siquirres road, 840 m elev., *Daniels & Stiles 40* (holotype, F!).

Herb 5–7 m tall. Leafy shoots in groups of 8 to 20; pseudostem 1.8–2.7 m tall, 6–7 cm in diameter; leaves 3 to 5 per shoot; petiole 1.3–1.6 cm long, 2–2.5 cm in diameter; longest blade 2–2.7 m by 45–55 cm. Inflorescence to 1.5 m long; peduncle yellow to red, woolly with yellow hairs, 30–55 cm long, 1.5–2.2 cm in diameter; rachis yellow to red, densely velutinous with yellow hairs, 1.5–2.1 cm in diameter at base; cincinnal bracts 25 to 35 per inflorescence, oriented 140–145° to axis of inflorescence, the middle bract with margins straight, inner surface pale yellow to orange and velutinous, outer surface red distally becoming yellow near rachis and velutinous, 9–10 cm long, 9–13 cm wide at base. Floral bracts 5.5 cm long, 2 cm wide at base. Flowers 15 to 25 per cincinnus; pedicel white to pink, glabrous, 1.2 cm long; perianth 6 cm long, 8–12 mm wide at base, at anthesis curved 70–90°; staminode 5–7 by 2–3 mm; ovary 1–1.2 cm by 6–7 mm. Drupes 1.5–1.7 cm by 9–11 mm.

SPECIMENS EXAMINED. **Costa Rica.** CARTAGO/LIMÓN: along road between Turrialba and Siquirres, elev. 2000–2500 ft, *Kress et al. 77-788* (DUKE). CARTAGO: road from Turrialba N to Pavones and Siquirres, elev. 600–700 m, *Lems 5054* (NY, US); beside Río Tepemechin, 4 km SE of Pejibaye, elev. 650 m, *Lent 3192* (F); forest near Río Tepemechin, elev. 800 m, *Lent 3737* (F); Chitaria, elev. 900 m, *Maas 755* (F). LIMÓN: along Hwy. 32 from Turrialba to Limón, ca. 11 mi S of Siquirres, elev. 650 m, *Croat 43326* (MO); near Guayacán, elev. 700 m, *Kress 76-611* (DUKE); along Hwy. CR 233, 15 km N of Tres Equis, elev. 300 m, *Lent 528* (F); Cimarrones, ca. 10 km E of Siquirres, margin of forested valley, elev. 200 m, *Maas 1134* (F, MO); along hwy. from Turrialba to Siquirres, *Sheffy 35* (CR); along hwy. to Siquirres near Chitaria, *Sheffy 89* (CR).

PHENOLOGY. Flowering throughout year; peaking late in dry season (February to April).

HABITAT AND DISTRIBUTION. Similar to the typical variety, var. *pubescens* is found in secondary growth and along forest margins. This variety is restricted to the Atlantic foothills in Costa Rica between Turrialba and Siquirres at elevations of 200–800 m (MAP 9).

RELATIONSHIPS. The velutinous to woolly peduncle, rachis, and cincinnal bracts distinguish var. *pubescens* from the other varieties of *Heliconia pogonantha*.

15d. **Heliconia pogonantha** var. **veraguasensis** Kress, J. Arnold Arbor. **62**: 256. 1981. TYPE: Panama, Veraguas, 2 mi above Santa Fé beyond Agricultural School, elev. 850 m, *Kress, Clarkson, & McDade 77-825* (holotype, DUKE!; isotypes, K!, MO!). PLATE VII, A, C.

Herb 4–4.5 m tall. Leafy shoots in groups of 3 to 15; pseudostem 1.3–1.7 m tall, 5 cm in diameter; petiole 1–1.2 m long, 1.5–1.8 cm in diameter; leaf blade with lower surface green tinted with maroon especially along margins, longest blade 1.2–1.5 m by 40–45 cm. Inflorescence to 75 cm long; peduncle yellow, scurfy to villous, 10–30 cm long, 1.8–2 cm in diameter; rachis yellow, puberulous to villous, 1.8–1.9 cm in diameter at base; cincinnal bracts 20 to 25 per inflorescence, oriented 115–135° to axis of inflorescence, the middle bract with margins straight, inner surface red-yellow and tomentose, outer surface red becoming yellow near rachis and glabrous to puberulous, 9–10.5 cm long, 8–9 cm wide at base. Floral bracts pale yellow, tomentose to velutinous with golden hairs abaxially, 4–4.8 cm long, 1.5–2.5 cm wide at base. Flowers 10 to 15 per cincinnus; pedicel white to yellow, puberulous, 7–12 mm long; perianth 5.4–5.7 cm long, 1–1.1 cm wide at base, at anthesis curved 80–90°; staminode 6–7 by 3 mm; ovary 8–9 by 5–6 mm.

SPECIMENS EXAMINED. **Panama.** VERAGUAS: vic. of Santa Fé, forested slopes of Cerro Tute, elev. 3000 ft, *Allen 4333* (MO); road between Santa Fé and Río Calovébora, 1.8 mi beyond Escuela Agrícola Alto Piedra, elev. 735 m, *Croat & Folsom 34255* (MO); shoulder of Cerro Tute, *Folsom & Edwards 3355* (MO); Cerro Tute, elev. 800–1350 m, *Knapp & Dressler 5438* (MO), *Sytsma & Antonio 2983* (MO), *Andersson & Sytsma 1277* (GB, S); beyond Escuela Agrícola, above Santa Fé, elev. 2600 ft, *Kress & Cooper-Smith 76-655* (DUKE), *76-656* (DUKE), elev. 2800–4600 ft, *Kress et al. 80-1189* (DUKE); beyond Santa Fé along road to Calovébora, Pacific slopes, elev. 2200 ft, *Kress et al. 80-1200* (DUKE), *Andersson & Sytsma 1288* (GB, S); lower montane wet forest 7 km W of Santa Fé, elev. 2900 ft, *Nee 11207* (US); Caribbean slope above Río Primero Brazo, *Liesner 959* (MO); Río Secundo Brazo, elev. 600–750 m, *Knapp & Dressler 5372* (MO), *Maas & Dressler 1673* (U).

PHENOLOGY. Flowering March to September; during most of year at least a few individuals reproductive.

HABITAT AND DISTRIBUTION. *Heliconia pogonantha* var. *veraguasensis* is known only from middle-elevation (735–1000 m) wet forests and secondary growth in the vicinity of Cerro Tute on the Pacific slopes in Veraguas, Panama (MAP 9).

RELATIONSHIPS. Variety *veraguasensis* is distinguished by its highly reflexed cincinnal bracts, its lower leaf surfaces tinted with maroon, and its overall stature smaller than in other varieties of *Heliconia pogonantha*.

16. **Heliconia ramonensis** Daniels & Stiles, Brenesia **15**(Supl.): 39. 1979. TYPE: Costa Rica, [Alajuela,] La Balsa, 11 mi N of San Ramón, elev. 1000 m, *Daniels, Kress, & Hutchison 111* (holotype, F!; isotypes, CR, US).
PLATE VII, C, D.

Herb with *Musa*-like habit, 4–6 m tall. Leafy shoots in groups of 2 to 10; pseudostem green to yellow to brown, glabrous to villous, 1–2 m tall, 4.5–8 cm in diameter; leaves 3 to 5 per shoot; petiole rusty green to green, glabrous, 1–1.8 m long, 1.1–2 cm in diameter; blade with the base unequal, obtuse to cordate, the apex acute to acuminate, the upper surface dark green, glabrous,

with midrib light green to yellow-green and glabrous, the lower surface green to maroon, glabrous, with midrib green to maroon and glabrous, the longest blade 1–2 m by 30–60 cm. Inflorescence pendent, to 90 cm long; peduncle pink to rose-red to red, glabrous to woolly with golden or rusty orange hairs, 20–60 cm long, 1.3–2 cm in diameter; rachis flexuose, red to pink to yellow, glabrous to woolly, 1–2.2 cm in diameter at base; cincinnal bracts distichous to subspirally arranged, 20 to 40 per inflorescence, oriented 120–140° to axis of inflorescence, the basal bract usually fertile, the middle bract with apex acute to acuminate, margins straight to involute at base, inner surface pink to red to yellow and velutinous to villous with golden or rusty hairs, outer surface red to rose-red to pink and glabrous to woolly, 7–12 cm long, 7–10 cm wide at base, l/w = 1.1. Floral bracts opaque, persistent, white to pink, glabrous to villous abaxially, 4–5 cm long, 1.5–3 cm wide at base. Flowers 10 to 30 per cincinnus; pedicel white to pink, glabrous, 0.7–3 cm long; perianth white to light pink and glabrous basally, yellow and velutinous toward apex, 4.5–5.6 cm long, 1–1.2 cm wide at base, at anthesis curved 60–90° and sigmoid; free sepal reflexed, fused sepals with apices reflexed; staminode white (sometimes with yellow apex), 6–10 by 2–4 mm, apex acuminate to cuspidate; stamens with anthers connivent inside corolla apex; pollen *pogonantha* type, large (60–63 × 78–88 μm), euoblate (P/E = 0.68–0.81), heteropolar (DR/PR = 5.79–8.7) with the distal hemisphere convex, truncate, spinulose, the proximal hemisphere planar, psilate, the germination aperture distinct, flattened, sunken; ovary white to pale blue to lavender, glabrous, 7–10 by 5–7 mm. Drupes glabrous, 1.3–1.5 cm by 8–10 mm; pyrenes 9 by 5 mm.

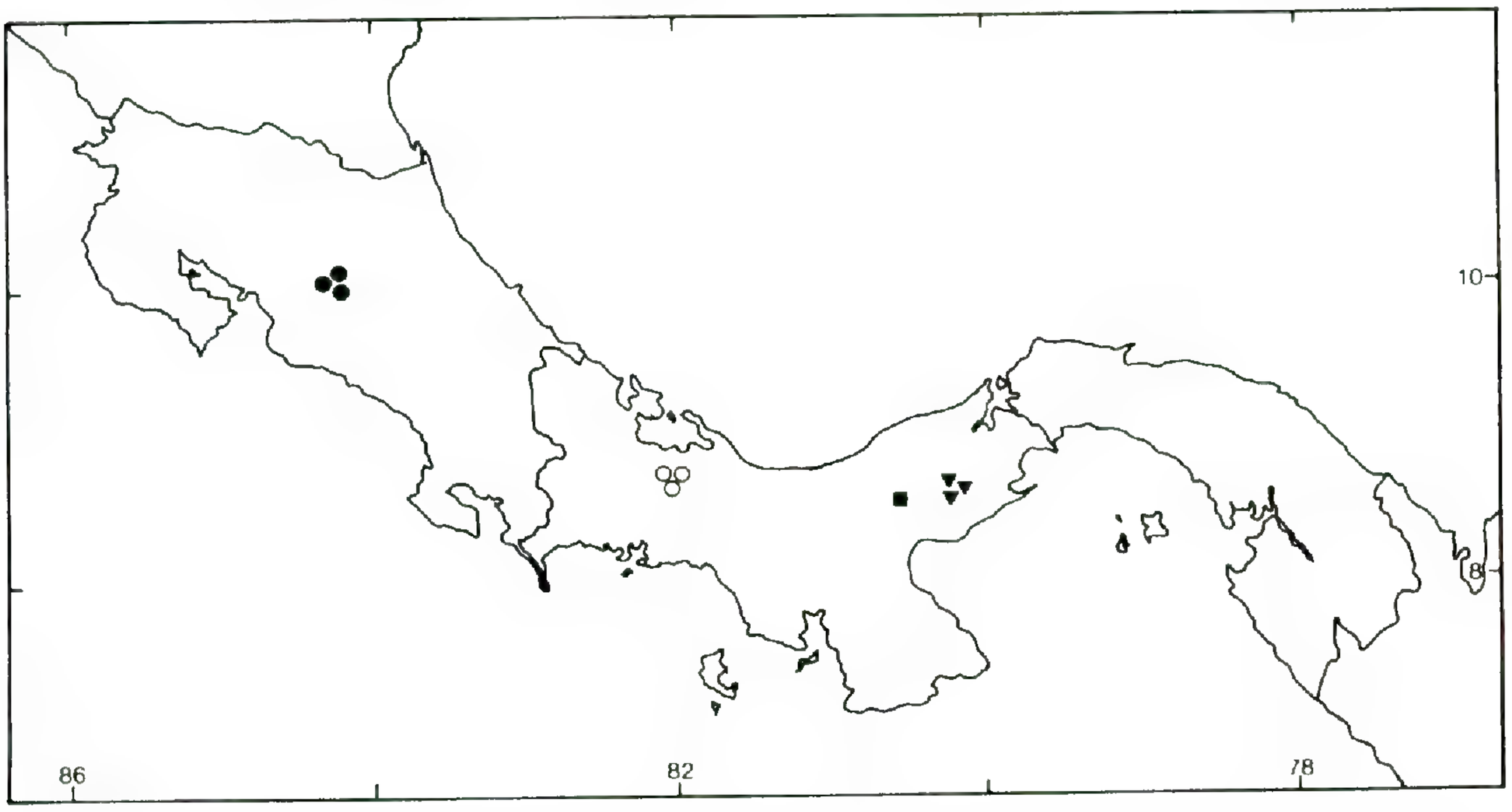
HABITAT AND DISTRIBUTION. *Heliconia ramonensis* occurs in middle-elevation (600–1200 m) forests of Costa Rica and Panama (MAP 10). Plants inhabit moist, forested slopes and often invade disturbed open areas.

VARIATION. The four varieties of *Heliconia ramonensis* are distinguished from each other by the distribution of the woolly vestiture on the peduncle, rachis, and cincinnal bracts, and by the color of the hairs on the floral bracts and perianth apices.

RELATIONSHIPS. *Heliconia ramonensis* belongs to the *pogonantha* group; it differs from other members of that group in the rusty orange hairs on various parts of its inflorescence and peduncle and in its bright pink to red cincinnal bracts.

Key to the Varieties of *Heliconia ramonensis*

A. Peduncle, rachis, and cincinnal bracts all essentially glabrous. . . . . 16c. var. *glabra.*
A. Peduncle, rachis, or cincinnal bracts villous to woolly.
  B. Peduncle, rachis, and cincinnal bracts all woolly. . . . . 16d. var. *lanuginosa.*
  B. Peduncle and sometimes rachis woolly, cincinnal bracts glabrous to villous.
    C. Vestiture on floral bracts and perianth pale yellow to buff; cincinnal bracts red. . . . . 16a. var. *ramonensis.*
    C. Vestiture on floral bracts and perianth bright yellow; cincinnal bracts rose-red to pink. . . . . 16b. var. *xanthotricha.*



MAP 10. Costa Rica and Panama, showing allopatric distribution of *Heliconia ramonensis* var. *ramonensis* (solid circles), var. *xanthotricha* (solid triangles), var. *glabra* (solid square), and var. *lanuginosa* (open circles).

16a. **Heliconia ramonensis** var. **ramonensis**

Herb to 5 m tall. Pseudostem 1.5–2 m tall, 4.5–6 cm in diameter; leaves with the petiole rusty green, 1.4–1.8 m long, 1.7–1.9 cm in diameter, the blade with base obtuse to truncate, the longest blade 1.6–2 m by 45–55 cm. Inflorescence to 85 cm long; peduncle red, woolly with golden hairs, 40–60 cm long, 1.8–2 cm in diameter; rachis red, villous to woolly with golden hairs, 1.5–2 cm in diameter at base; cincinnal bracts 20 to 30 per inflorescence, the middle bract with inner surface villous with golden hairs, outer surface red to pink-red and puberulous to scurfy, 9–10 cm long, 8–10 cm wide at base. Floral bracts pink, glabrous to villous with golden hairs abaxially, 4–5 cm long, 1.5–3 cm wide at base. Flowers 20 to 30 per cincinnus; pedicel 1.2–3 mm long; perianth glabrous basally, villous with golden hairs toward apex, 4.5–5.5 cm long, 1–1.2 cm wide at base; staminode white, yellow at apex, 7–10 by 3–4 mm; ovary pale lavender, 7–10 by 6–7 mm. Drupes not seen.

SPECIMENS EXAMINED. **Costa Rica.** ALAJUELA: Cataratas de San Ramón, *Brenes 18370* (CR); 15 mi from San Ramón near La Balsa, elev. 1000 m, *Kress et al. 76-604* (DUKE), *77-764* (DUKE); entre Balsa de San Ramón y Río Cataratas, ca. 12 km N of La Balsa, elev. 550–1100 m, *Utley & Utley 3745* (DUKE).

PHENOLOGY. Flowering primarily during early rainy season (July to September); some inflorescences produced throughout year.

DISTRIBUTION. *Heliconia ramonensis* var. *ramonensis* is endemic to Costa Rica in the foothills (ca. 1000 m) above San Ramón (MAP 10).

16b. **Heliconia ramonensis** var. **xanthotricha** Kress, J. Arnold Arbor. **62**: 258. 1981. TYPE: Panama, Coclé, 6 mi beyond El Valle de Antón behind Cerro Gaital, elev. 900 m, *Kress, Clarkson, & McDade 77-840* (holotype, DUKE!; isotypes, K!, MO!).

Heliconia vellerigera auct. non Poeppig: Woodson & Schery, Ann. Missouri Bot. Gard. **32:** 55. 1945, in part (Woodson & Schery included *H. magnifica* and *H. ramonensis* in *H. vellerigera*).

Herb 4–5 m tall. Leafy shoots in groups of 3 to 10; pseudostem orange to brown, 1.3–2 m tall, 5–8 cm in diameter; leaves with the petiole green, 1–1.2 m long, 1.5–2 cm in diameter, the blade with base truncate to cordate, lower surface green tinted with maroon especially along margins, the longest blade 1.3–1.8 m by 40–60 cm wide. Inflorescence to 90 cm long; peduncle red, woolly with golden-yellow hairs, 30–50 cm long, 1.6–2 cm in diameter; rachis red-orange, velutinous to villous with yellow hairs, 1.5–2.2 cm in diameter at base; cincinnal bracts 20 to 40 per inflorescence, oriented 135–140° to axis of inflorescence, the middle bract with inner surface pink and velutinous to villous, outer surface rose-red, 9–12 cm long, 7–10 cm wide at base. Floral bracts white to pink, velutinous to villous with bright yellow hairs abaxially. Flowers 10 to 15 per cincinnus; pedicel 7–13 mm long; perianth glabrous basally, tomentose to velutinous with bright yellow hairs toward apex, especially along sepal margins, 5–6 cm long, 1–1.2 cm wide at base, at anthesis curved 90°; staminode 7–8 by 2–3 mm; ovary bluish white, 8–10 by 5–6 mm. Drupes 1.3–1.5 cm by 9–10 mm.

SPECIMENS EXAMINED. **Panama.** COCLÉ: base of three peaks beyond El Valle de Antón, elev. 800 m, *Kress & Cooper-Smith 76-651* (DUKE), *Kress & Hammel 83-1581* (DUKE), *Maas et al. 1725* (MO, U, US), elev. 800–1000 m, *Allen 1818* (MO), elev. 2500–3000 ft, *Lewis et al. 1750* (MO), *Luteyn & Kennedy 1718* (DUKE, MO); on trail to Las Minas, elev. 1000 m, *Allen 2707* (MO), *Allen 2867* (US); vic. Finca Tomas Arias, elev. 600 m, *Allen 3629* (US); foot of Cerro Pilón, elev. 2000 ft, *Porter et al. 4423* (SCZ, UC), *Croat 13471* (MO); La Mesa, 2.8–3.4 mi NW of El Valle de Antón, elev. 850–900 m, *Luteyn 4064* (DUKE), *Croat 25311* (MO), elev. 900 m, *Croat 14374* (MO, SCZ), *22952* (MO), *Antonio 1292* (MO), elev. 900 m, *Sullivan 541* (MO), *D'Arcy & Sytsma 14665* (MO); ca. 9 km from El Valle Market beyond Sr. Furlong's Finca, *Kennedy et al. 3223* (DUKE, MO); Cerro Gaital, N of El Valle, elev. 760 m, *Reveal & Balogh 4971* (MO), elev. 2200 ft, *Kress et al. 80-1161* (DUKE); near Cerro Turega, elev. 650–700 m, *Woodson & Schery 205* (MO); Cerro Caracoral, elev. 2700–3200 ft, *Sytsma 3764* (MO), *3799* (MO), *4053* (MO), *Andersson & Sytsma 1249* (S).

PHENOLOGY. Flowering mainly during rainy season (May to September); some inflorescences produced throughout year.

DISTRIBUTION. In Central America *Heliconia ramonensis* var. *xanthotricha* is found at middle elevations (650–1000 m) in Coclé, Panama, in the region around El Valle de Antón (MAP 10).

RELATIONSHIPS. Variety *xanthotricha* differs from vars. *ramonensis* and *lanuginosa* in the bright yellow vestiture on its floral bracts and perianth apices (also found in var. *glabra*), and in the contrasting colors of its red-orange rachis and rose-red cincinnal bracts.

16c. **Heliconia ramonensis** var. **glabra** Kress, var. nov.

A var. ramonensi inflorescentiis glabris et floribus pubescentiis luteis differt.

TYPE: Panama, Coclé, beyond sawmill above El Copé, elev. 2400 ft, *Kress & Hammel 83-1589* (holotype, DUKE!; isotype, MO!).

Herb 4–5 m tall. Leafy shoots in groups of 5 to 10; pseudostem green and brown, glabrous, 1–1.5 m tall, 5–7 cm in diameter; leaves with the petiole green, 1–1.2 m long, 1.1–1.5 cm in diameter, the blade with base cordate, apex acute, lower surface tinted maroon with maroon lateral venation and green midrib, the longest blade 1.1–1.3 m by 30–40 cm. Inflorescence to 50 cm long; peduncle rose-red, glabrous, 20–30 cm long, 1.3–1.5 cm in diameter; rachis rose-red, glabrous to scurfy, 1–1.3 cm in diameter at base; cincinnal bracts 20 to 30 per inflorescence, oriented 135° to axis of inflorescence, the middle bract with inner surface pink and velutinous with yellow hairs, outer surface rose-red to pink and glabrous, 7–8 cm long, 7–9 cm wide at base. Floral bracts white, villous with bright yellow hairs abaxially, 5 cm long, 2 cm wide at base. Flowers 25 per cincinnus; pedicel pink, 1 cm long; perianth with bright yellow hairs toward apex, 5.6 cm long, 1.2 cm wide at base, at anthesis curved 85°; staminode 6 by 2 mm; ovary white, 8 by 6 mm. Drupes not seen.

SPECIMENS EXAMINED. **Panama.** COCLÉ: area surrounding Rivera sawmill, 7 km N of El Copé, continental divide, elev. 750–860 m, *Folsom & Collins 6430* (DUKE, MO).

PHENOLOGY. Apparently flowering mainly during rainy season (July to November).

DISTRIBUTION. Although quite common at the type locality (pers. obs.), var. *glabra* has been collected only a few times and appears to be restricted to the mountains (750–850 m) above El Copé in Coclé, Panama (MAP 10).

RELATIONSHIPS. This variety is quite different from the other varieties of *Heliconia ramonensis* in its entirely glabrous peduncle, rachis, and cincinnal bracts. The bright yellow hairs of the floral bracts and perianths are also present in var. *xanthotricha*.

16d. **Heliconia ramonensis** var. **lanuginosa** Kress, var. nov. PLATE VII, B, D.

A var. ramonensi inflorescentiis omnibus lanuginosis et pubescentia ferruginea differt.

TYPE: Panama, Chiriquí, La Fortuna Dam site above Gualaca, elev. 3600 ft, *Kress & Hammel 83-1602* (holotype, DUKE!; isotypes, K!, MO!, PMA!).

Herb 5–6 m tall. Leafy shoots in groups of 2 to 5; pseudostem yellow to brown, glabrous to villous, 2 m tall, 5–6 cm in diameter; leaves with the petiole green and maroon, 1–1.2 m long, 1.6–1.8 cm in diameter, the blade with base truncate to cordate, lower surface green (sometimes with maroon borders), the longest blade 1.6–1.8 m by 37–44 cm. Inflorescence to 75 cm long; peduncle pink, woolly with rusty orange hairs, 20–50 cm long, 1.5–1.7 cm in diameter; rachis pink to pale yellow, woolly with rusty orange hairs, 1.4 cm in diameter at base; cincinnal bracts 20 to 25 per inflorescence, oriented 120–135° to axis of inflorescence, the middle bract with inner surface pale yellow and villous to velutinous with rusty orange hairs, outer surface pink to rose-red and villous to woolly with rusty orange hairs, 10–11 cm long, 7–9 cm wide at base. Floral bracts white, velutinous with rusty orange hairs abaxially, 4–4.5 cm long, 1.9–2 cm wide at base. Flowers 20 per cincinnus; pedicel white, 5–8 mm long;

perianth light pink basally, velutinous with rusty orange hairs apically, 5–5.5 cm long, 1.2 cm wide at base, at anthesis curved 90°; staminode white with yellow apex, 8–9 by 2 mm, apex acuminate; ovary white, 6–10 by 5 mm.

SPECIMENS EXAMINED. **Panama.** CHIRIQUÍ: along road between Gualaca and Fortuna Dam site, 7.9 mi NW of Los Planes de Hornito, elev. 1300 m, *Antonio 4130* (MO); N del sitio de presa de Fortuna, elev. 1000–1200 m, *Correa et al. 2317* (MO), *2670* (MO); Fortuna Dam site, elev. 1040 m, *Hammel 1989* (MO), elev. 1000–1200 m, *Kress et al. 82-1350* (DUKE), *Kress & Hammel 83-1600* (DUKE), elev. 1200–1400 m, *Folsom et al. 5493* (MO). BOCAS DEL TORO: Atlantic slopes beyond La Fortuna Dam site, elev. 1000 m, *Kress & Hammel 83-1604* (DUKE).

PHENOLOGY. Flowering mainly during rainy season (May to September).

DISTRIBUTION. Variety *lanuginosa* has been collected in the mountains (1000–1300 m) surrounding the Fortuna Hydroelectric Dam project in Chiriquí and neighboring Bocas del Toro, Panama (MAP 10).

RELATIONSHIPS. The inflorescences of this variety are conspicuously different from those of the other varieties in being entirely covered with a woolly indumentum of rusty orange hairs. In vars. *ramonensis* and *xanthotricha* this rusty vestiture is restricted mainly to the peduncle and rachis. The rusty orange hairs on the floral bracts and perianth of var. *lanuginosa* differ from the yellow hairs of the other varieties.

17. **Heliconia danielsiana** Kress, sp. nov. FIGURE 13; PLATE VIII, A, D.

Heliconia vellerigera auct. non Poeppig: Daniels & Stiles, Brenesia **15**(Supl.): 45. 1979.

Planta herbacea, 4.5–8 m alta; inflorescentia pendens, rubra, pubescentia lanata aurantiaca usque ad bubalinam; cincinnorum bracteae distichae vel subspirales; perianthium basi album apice lutescens, apice pubescentia cinnamomea usque ad bubalinum; ovarium album glabrum; fructus caeruleus glaber.

TYPE: Costa Rica, San José, 15 km above Dominical on road to San Isidro, elev. 2800 ft, *Kress & Clarkson 79-1097* (holotype, DUKE!; isotypes, CR!, F!).

Herb with *Musa*-like habit, 4.5–8 m tall. Leafy shoots in groups of 5 to 15; pseudostem brown, scurfy to villous, 1.8–3 m tall, 5–8 cm in diameter; leaves 2 to 4 per shoot; petiole green to yellow, glabrous, 1–1.8 m long, 2–2.5 cm in diameter; blade with the base unequal, truncate to cordate, the apex acute, the upper surface green to dark green, glabrous, with midrib green to yellow and glabrous, the lower surface green, slightly glaucous, midrib green to yellow with maroon midstripe and glabrous, the longest blade 2–2.8 m by 45–57 cm. Inflorescence pendent, to 1 m long; peduncle orange to red, woolly with orange (when fresh) to buff (when dried) hairs, 10–40 cm long, 1.6–2 cm in diameter; rachis flexuose, orange to red, woolly, 1.6–2 cm in diameter at base; cincinnal bracts distichous to subspirally arranged, 20 to 30 per inflorescence, oriented 130–150° to axis of inflorescence, the basal bract usually fertile, the middle bract with apex acute to acuminate, margins straight to involute, inner surface pink and velutinous, outer surface orange-red and woolly with orange (when

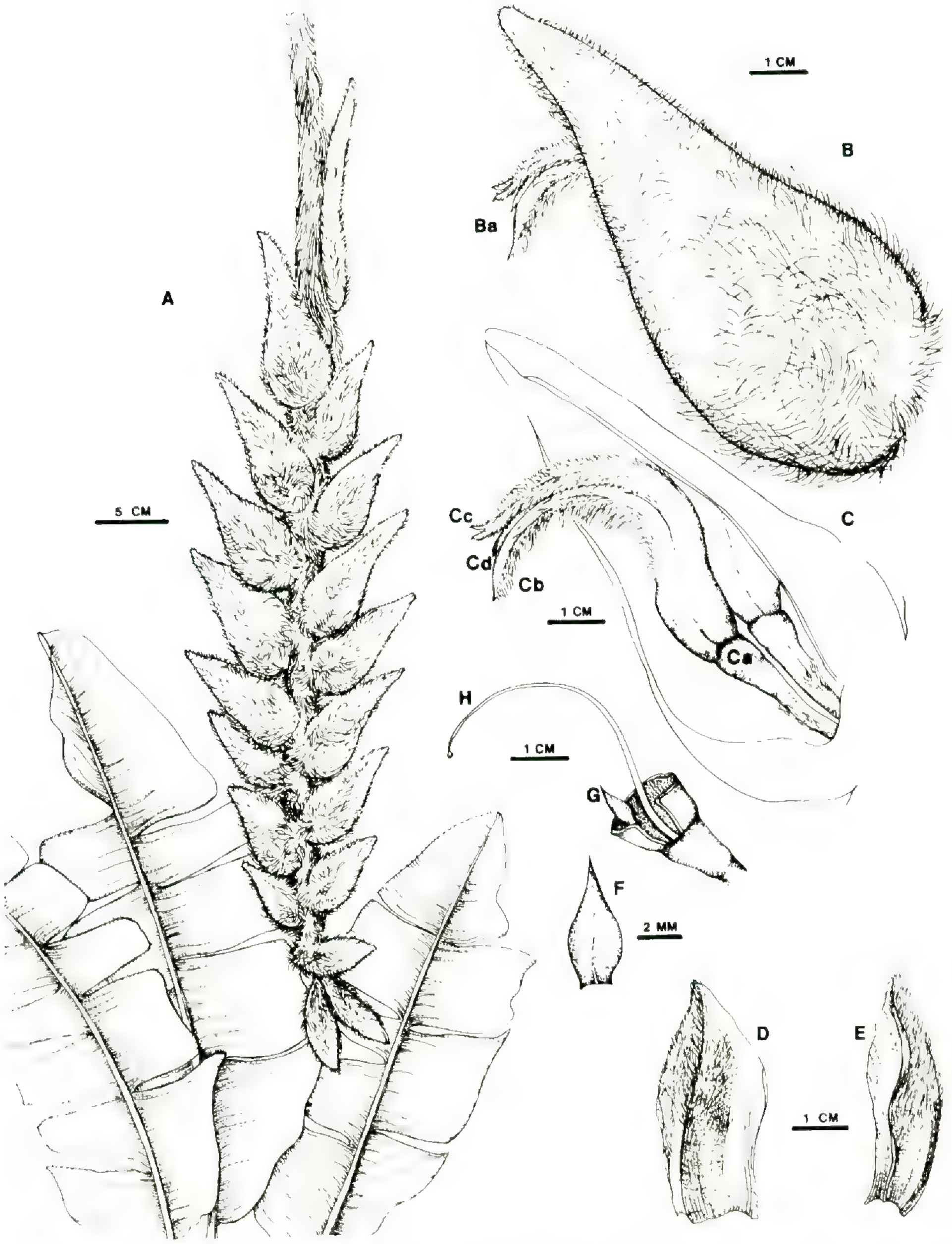
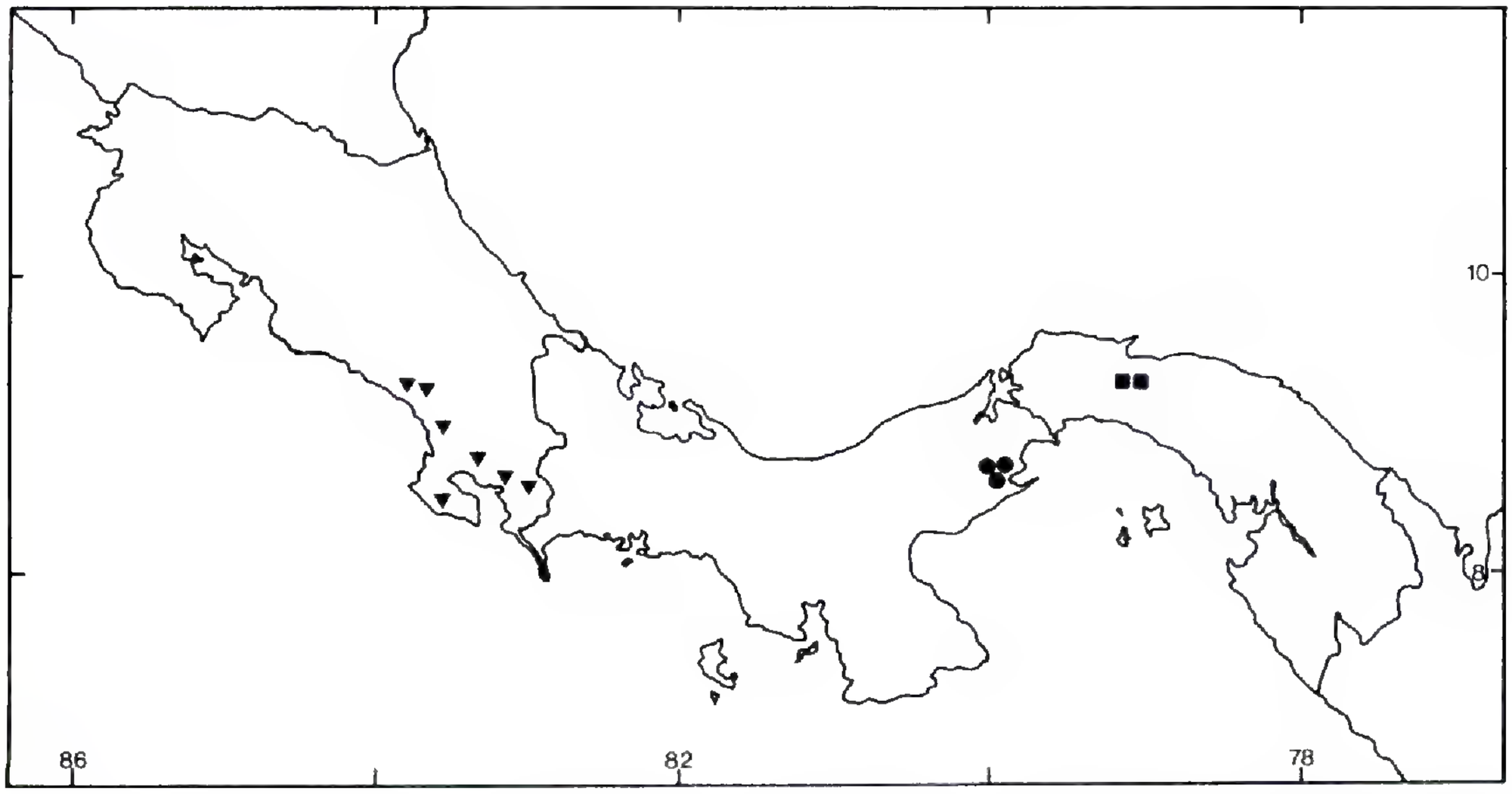


FIGURE 13. *Heliconia danielsiana*. A, inflorescence. B, C, cincinnal bracts: B, entire (Ba, flower protruding at anthesis); C, cut-away, floral bracts removed showing flower at anthesis (Ca, ovary; Cb, free sepal; Cc, fused sepals, slightly reflexed; Cd, anthers, included in apex of corolla tube). D, E, floral bracts: D, abaxial view; E, lateral view. F, G, staminode: F, abaxial view; G, position relative to style, lateral view. H, style and stigma.

fresh) to buff (when dried) hairs, 9.5–11 cm long, 8–10 cm wide at base, l/w = 1.1. Floral bracts opaque, persistent, white to pink, velutinous to villous with golden hairs abaxially, 4–5 cm long, 2–2.5 cm wide at base. Flowers 15 to 20 per cincinnus; pedicel white to pink, glabrous to puberulous, 9–12 mm long; perianth white and glabrous basally, yellow and velutinous with cinnamon to



MAP 11. Costa Rica and Panama, showing allopatric distribution of *Heliconia danielsiana* (triangles), *H. magnifica* (circles), and *H. xanthovillosa* (squares).

buff hairs apically, 5.1–5.7 cm long, 1–1.2 cm wide at base, at anthesis curved 85–90° and sigmoid; free sepal slightly reflexed, fused sepals with apices slightly reflexed; staminode white with yellow apex, 5–7 by 2–3 mm, apex acuminate; stamens with anthers connivent inside perianth apex; pollen *pogonantha* type, large (60 × 86 μm), euoblate (P/E = 0.71), heteropolar (DR/PR = 7.9) with the distal hemisphere convex, truncate, spinulose, the proximal hemisphere planar, psilate, the germination pore distinct, flattened, sunken; ovary white, glabrous, 8–10 by 5–6 mm. Drupes glabrous.

SPECIMENS EXAMINED. **Costa Rica.** PUNTARENAS: Golfo Dulce area, vic. Esquinas Experiment Station, sea level, *Allen 5235* (US); entre Los Ríos Piedras Blancas y Esquinas, Osa, elev. 75 m, *Jiménez 2248* (F, GH, NY); Esquinas Forest Reserve between Palmar and Río Claro, elev. ca. 100 ft, *Kress et al. 76-589* (DUKE), *Kress 78-1046* (DUKE); forest 30 km SE of Palmar Sur on Pan Am Hwy., *Lent 171* (CR); forest of Río Convento, 36 km S of San Isidro del General, elev. 500 m, *Molina et al. 17980* (NY); 8 mi from Villa Neily on road to San Vito, elev. 3500 ft, *Kress et al. 77-821* (DUKE); San Vito de Java, cult. at Las Cruces Trop. Bot. Garden, elev. ca. 4000 ft, *Kress 76-575* (DUKE), *78-1031* (DUKE); Golfito, along trail to TV tower, steep forested slopes, elev. 100–300 m, *Burger & Matta 4772* (CR), *4773* (CR, F, GH, US); Península de Osa, Corcovado Natl. Park, elev. 20–400 m, *Liesner 3177* (MO); Península de Osa, Camino de Altura, 2–5 mi W of Rincón de Osa, elev. 400–1000 ft, *Raven 21494* (CR, F). SAN JOSÉ: El General Valley, vic. of San Isidro del General, elev. 500 m, *Molina et al. 17980* (F); between San Isidro and Playa Dominical, *Sheffy 62* (CR).

PHENOLOGY. Flowering throughout year, with slight peak in early rainy season (June to August).

HABITAT AND DISTRIBUTION. *Heliconia danielsiana* is restricted to Costa Rica, where it occurs only on the Pacific slopes from Dominical to the Golfo Dulce area (MAP 11). This species inhabits open disturbed areas from sea level to 1200 m.

RELATIONSHIPS. This species, a member of the *pogonantha* group, has extremely woolly inflorescences. It is distinguished by its orange-red cincinnal bracts and by the orange to buff vestiture densely covering the entire inflorescence.

NOMENCLATURE. Daniels and Stiles (1979) applied the name *Heliconia vellerigera* Poeppig to the Costa Rican species characterized by an extremely woolly vestiture covering the entire pendent inflorescence. Indeed, Poeppig had described such a plant from Peru and deposited a type at Vienna (W). The type specimen is minimal, consisting only of several cincinnal bracts, and does not have any flowers or leaves. Other collections seen from Peru (e.g., *Ferreyra 1198,* US; *Berlin 383,* F; *Plowman & Schunke 11471,* DUKE, F) and Colombia (*Foster & Foster 2270,* GH) with similar woolly inflorescences have glabrous flowers that differ from the velutinous flowers of plants found in Costa Rica. The large geographic distance between the type locality of *H. vellerigera* and Costa Rica and the difference in the vestiture of the flowers leave no doubt that the plants found in Costa Rica are specifically distinct from Poeppig's taxon. The specific epithet proposed here honors Dr. Gilbert S. Daniels, who has contributed much to our understanding of the *Heliconia* taxa of Costa Rica, and who first showed me the new species in its native habitat.

18. **Heliconia magnifica** Kress, J. Arnold Arbor. **62:** 246. 1981. TYPE: Panama, Panamá, Cerro Campana, beyond Su Lin Motel, elev. 1000 m, *Kress, Clarkson, & McDade 77-850* (holotype, DUKE!; isotypes, K!, MO!).
FIGURE 14; PLATE VIII, B, E.

Heliconia vellerigera auct. non Poeppig: Woodson & Schery, Ann. Missouri Bot. Gard. **32:** 54. 1945, in part (Woodson & Schery included *H. magnifica* and *H. ramonensis* var. *xanthotricha* in *H. vellerigera*).

Herb with *Musa*-like habit, 4–6 m tall. Leafy shoots solitary or in groups of 2 to 5; pseudostem rusty brown, scurfy to villous, 1.1–2.3 m tall, 3–7 cm in diameter; leaves 3 or 4 per shoot; longest petiole light green and maroon, glabrous, 1.1–1.8 m long, 1–1.9 cm in diameter; blades splitting into narrow lateral segments with age, the base unequal, truncate to cordate, the apex acute, the upper surface dark green, glabrous, with midrib yellow-green and glabrous, the lower surface green with maroon margins, glabrous, with midrib yellow-green and glabrous, the longest blade 1.1–1.9 m by 36–55 cm. Inflorescence pendent, to 94 cm long; peduncle dark red to burgundy, woolly with golden to burgundy hairs, 30–50 cm long, 1–1.7 cm in diameter; rachis flexuose, twisted, red to burgundy, woolly, 1–1.6 cm in diameter at base; cincinnal bracts spirally arranged, up to 35 per inflorescence, oriented 130–150° to axis of inflorescence, the basal bract usually fertile, the middle bract with apex acuminate, margins straight becoming involute at base, inner surface white to red and pubescent to velutinous, outer surface red to burgundy and villous to woolly with burgundy hairs, 8–10 cm long, 7.5–9.5 cm wide at base, l/w = 1.1. Floral bracts opaque, persistent, pink, velutinous abaxially, 3.5–5 cm long, 1–1.5 cm wide at base. Flowers 10 to 15 per cincinnus; pedicel white, pink near ovary, glabrous, 1–1.3 cm long; perianth white and glabrous basally, yellow and velutinous with

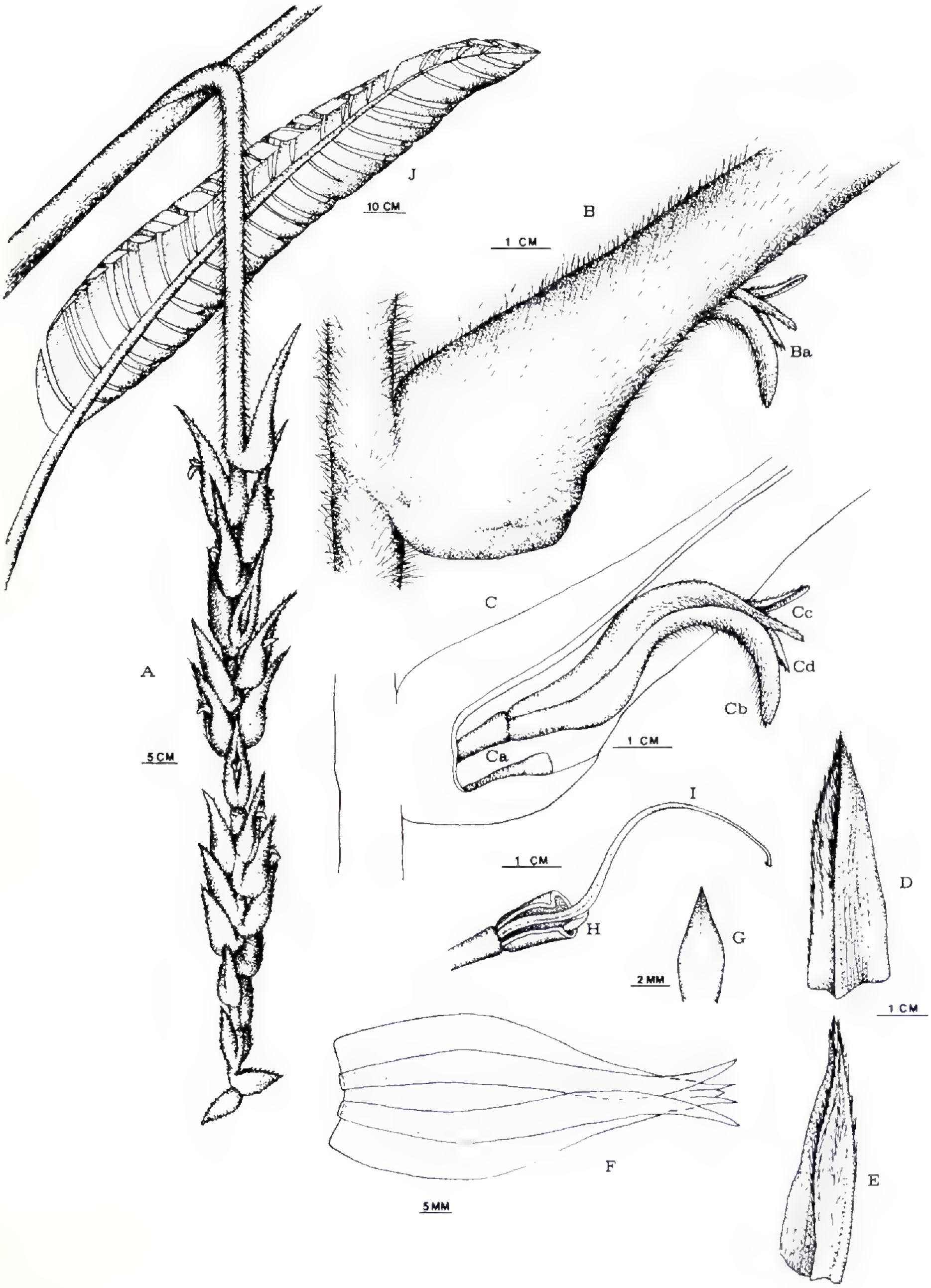


FIGURE 14. *Heliconia magnifica*. A, inflorescence. B, C, cincinnal bracts: B, entire (Ba, flower protruding at anthesis); C, cut-away, floral bracts removed showing flower at anthesis (Ca, ovary; Cb, free sepal; Cc, fused sepals, partially reflexed; Cd, anthers, included in apex of corolla tube). D, E, floral bracts: D, abaxial view; E, lateral view. F, perianth, outer surface showing 2 sepals fused to partially spread-open corolla tube. G, H, staminode: G, abaxial view; H, position relative to style, lateral view. I, style and stigma. J, mature leaf, blade split into lateral segments.

golden hairs toward apex, 5.5–6 cm long, 1–1.2 cm wide at base, at anthesis curved 80–90° and sigmoid; free sepal reflexed, fused sepals with apices slightly reflexed; staminode white, yellow at apex, 5–6 by 2–3 mm, apex acuminate; stamens with anthers connivent inside apex of corolla tube; pollen *pogonantha* type, large (65 × 82 μm), suboblate (P/E = 0.78), heteropolar (DR/PR = 6.07) with the distal hemisphere convex, truncate, spinulose, the proximal hemisphere planar, psilate, the germination aperture distinct, flattened, sunken; ovary white, glabrous, 1–1.1 cm by 5–6 mm. Drupes glabrous, 1.2–1.3 cm by 8–10 mm; pyrenes 9 by 6 mm.

SPECIMENS EXAMINED. **Panama.** PANAMÁ: Cerro Campana, elev. 600 m, *Antonio 1250* (MO), *1725* (MO), *4855* (MO), elev. 700–800 m, *Andersson 1317* (GB, S), elev. 850 m, *Busey 847* (MO), *Liesner 627* (F, MO, NY), elev. 875 m, *Croat 25239* (MO), elev. 2600–2800 ft, *Lewis et al. 1903* (MO), elev. 800–1000 m, *Gentry 4955* (F, MO, SCZ), elev. 1000 m, *Allen 2425* (MO, S), near summit, elev. 1000 m, *Kress & Cooper-Smith 76-648* (DUKE), elev. 2800 ft, *Sytsma 1233* (MO), elev. 2700–3200 ft, *Hammel 3783* (MO), elev. 3300 ft, *Kress 80-1246* (DUKE), ¾ of way to summit from Pan American Hwy., *Dwyer et al. 4850* (MO), cloud forest, *Luteyn & Kennedy 1814* (DUKE), without further location, *C. E. Smith & H. M. Smith 3399* (US).

PHENOLOGY. Flowering mainly March to September; some mature inflorescences all year.

HABITAT AND DISTRIBUTION. This species is found at middle elevations in the understory of cloud forest. It is endemic to Cerro Campana in Panama at elevations above 600 m (MAP 11).

RELATIONSHIPS. *Heliconia magnifica* is closely related to other species of the *pogonantha* group with large pendent woolly inflorescences, including *H. danielsiana, H. ramonensis,* and *H. xanthovillosa,* found in Central America. It is distinguished from these species by the dark red to burgundy color of its inflorescence and the red to golden woolly pubescence covering its peduncle, rachis, and cincinnal bracts.

19. **Heliconia xanthovillosa** Kress, J. Arnold Arbor. **62:** 253. [21 Aug.] 1981. TYPE: Panama, Panamá, El Llano–Cartí Road, 12 km from intersection with Pan American Hwy., elev. 500 m, *Kress & Knapp 80-1233* (holotype, DUKE!; isotypes, F!, GH!, K!, MO!, PMA!).

FIGURE 15; PLATE VIII, C, F.

Heliconia dresslerana Abalo & Antonio, Baileya **21:** 139. [17 Sept.] 1981. TYPE: Panama, Panamá, El Llano–Cartí Road, 15 km N of Panamerican Hwy. at El Llano, *Antonio 5258* (holotype, MO!; isotypes, PMA, US).

Herb with *Musa*-like habit, 3.5–4.5(–7) m tall. Leafy shoots in groups of 2 to 11; pseudostem brown, scurfy to puberulous, 1.6–1.9(–3.5) m tall, 6–7 cm in diameter; leaves 4 per shoot; petiole dull green, glabrous, 1.1–1.2 m long, 1.9–2(–2.5) cm in diameter; blade with the base unequal, obtuse to truncate, the apex acute, the upper surface green to dark green, glabrous, with midrib light green and glabrous, the lower surface green, glabrous, with midrib yellow-green and glabrous, the longest blade 1.9–2.3 m by 49–55 cm. Inflorescence

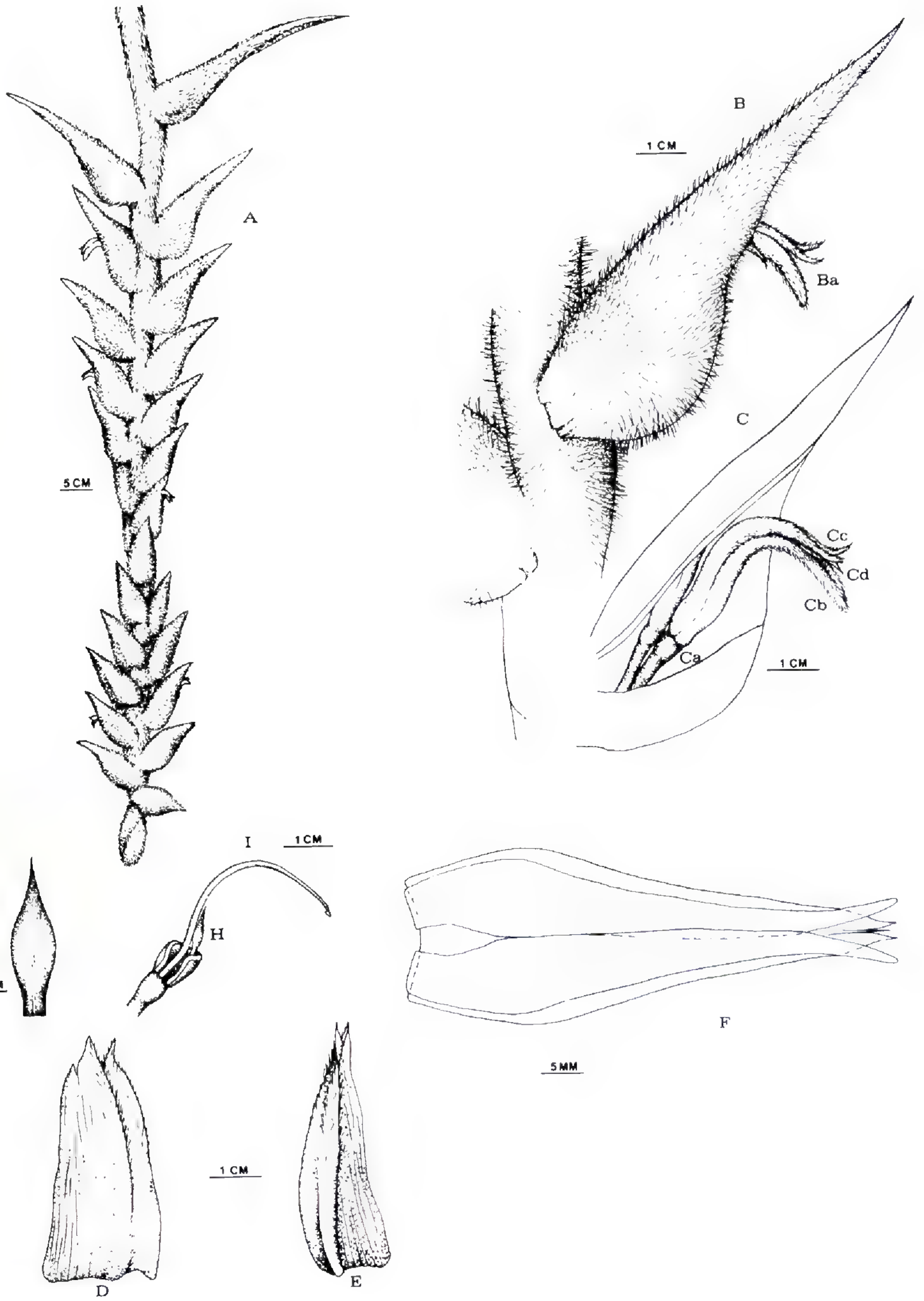


FIGURE 15. *Heliconia xanthovillosa*. A, inflorescence. B, C, cincinnal bracts: B, entire (Ba, flower protruding at anthesis); C, cut-away, floral bracts removed showing flower at anthesis (Ca, ovary; Cb, free sepal; Cc, fused sepals, slightly reflexed; Cd, anthers, included in apex of corolla tube). D, E, floral bracts: D, abaxial view; E, lateral view. F, perianth, outer surface showing 2 sepals fused to partially spread-open corolla tube. G, H, staminode: G, abaxial view; H, position relative to style, lateral view. I, style and stigma.

pendent, to 86(–105) cm long; peduncle bright yellow-green, woolly with yellow hairs, 26–68 cm long, 1.5–2.2 cm in diameter; rachis flexuose, bright yellow, woolly with yellow hairs, 1.5–1.9 cm in diameter at base; cincinnal bracts distichous to subspirally arranged, up to 35 per inflorescence, oriented 135–145° to axis of inflorescence, the basal bract sterile or fertile, the middle bract with apex acuminate to acute, margins straight to involute at base, inner surface pale yellow-green (sometimes pink) and villous, outer surface bright yellow to green-yellow (sometimes red distally) and woolly with yellow hairs, 8–10 cm long, 7–8 cm wide at base, l/w = 1.2. Floral bracts opaque, persistent through fruiting, pale yellow, velutinous to villous abaxially, 3.7–4.8 cm long, 1.6–1.7 cm wide at base. Flowers 12 to 20 per cincinnus; pedicel white, glabrous (to hirsute with yellow hairs), 1 cm long; perianth white and glabrous basally, yellow and velutinous to villous with bright yellow hairs distally, 5.1–5.5 cm long, 9–11 mm wide at base, at anthesis curved 85–90° and sigmoid; free sepal reflexed, fused sepals with apices slightly reflexed; staminode white, 5(–8) by 3(–5) mm, apex acuminate; stamens with anthers connivent inside apex of corolla tube; pollen *pogonantha* type, large (65 × 81 μm), suboblate (P/E = 0.79), heteropolar (DR/PR = 6.63), with the distal hemisphere convex, truncate, spinulose, the proximal hemisphere planar, psilate, the germination aperture distinct, flattened, sunken; ovary white, glabrous, 7–8 by 5–6 mm. Drupes glabrous, 1.1–1.2 cm by 8 mm; pyrenes 8–9 by 5–6 mm.

SPECIMENS EXAMINED. **Panama.** PANAMÁ: El Llano–Cartí Road, 8 mi from Pan American Hwy., elev. 1200 ft, *Antonio 1699* (MO), elev. 300–500 m, *Folsom & Maas 5214* (MO), *Antonio 1266* (MO), *1277* (MO), *Folsom 3507* (MO), *Maas et al. 2810* (GB), *Andersson & Sytsma 1262* (GB, S), *Knapp et al. 4747* (MO), *Kress & Hammel 82-1335* (DUKE), *83-1564* (DUKE), *83-1565* (DUKE), *Kress & Knapp 80-1235* (DUKE).

PHENOLOGY. Flowering during rainy season (May to October); fruiting probably well into November.

HABITAT AND DISTRIBUTION. This species is found at middle elevations (300–500 m) in open areas in the forest, and now especially in areas disturbed by man. It has been collected only along the continental divide separating the drier Pacific slopes from the wetter Atlantic ones in eastern Panama above the Río Cartí (MAP 11).

VARIATION. Several individuals having large, stout inflorescences with yellow and red cincinnal bracts (*Antonio 1277*; *Kress & Knapp 83-1235*; *Kress & Hammel 82-1335, 83-1564*) have been collected on El Llano–Cartí Road. Although differing in bract color, the inflorescences are covered with the same yellow vestiture as typical *Heliconia xanthovillosa* and are thus considered a color form of that species.

RELATIONSHIPS. *Heliconia xanthovillosa* is closely related to species of the *pogonantha* group, especially *H. danielsiana, H. ramonensis,* and *H. magnifica,* which differ from each other essentially in cincinnal-bract and indumentum color. *Heliconia xanthovillosa* has bright yellow inflorescences that are entirely covered with long, yellow hairs.

Insufficiently Known Taxon

In the examination of numerous herbarium specimens, several collections from Panama (one from the Burica Peninsula in Chiriquí and two from Darién) have proved quite difficult to assign to any of the taxa of *Heliconia* with pendent inflorescences included here. These specimens have a characteristic inflorescence with a strongly flexuose rachis and nearly overlapping cincinnal bracts. The cincinnal bracts are distinctive in having apparently necrotic apices that are either black or green (due to algal growth?). Dodson and Gentry (1978) have described a species from Ecuador, *H. nigripraefixa,* that has the same feature. I do not think that these specimens should be placed in that taxon until further comparative studies can be made on living specimens in the field.

Specimens examined. **Panama.** Chiriquí: Península de Burica, 20 km W of Puerto Armuelles, elev. 400–600 m, *Busey 551* (MO). Darién: headwater of Río Tuquesa, ca. 2 km from continental divide, vicinity gold-mining camp of Tyler Kittredge, *Croat 27140* (MO), *27141* (MO).

Natural Hybrids

Natural hybrids are rare in *Heliconia.* As discussed earlier, attempts to artificially hybridize a wide range of heliconias have proved unsuccessful. Strong physiological stigma/style barriers to foreign pollen penetration are present in most species (Kress, 1981b, 1983b). Although a limited number of hybrids have been found involving species with pendent inflorescences (Table 7), only two—*H. curtispatha* × *H. pogonantha* var. *holerythra* and *H. mariae* × *H. pogonantha* var. *holerythra*—are known to occur in more than one locality. Detailed morphological descriptions and comparisons of the three parent taxa and their two hybrid offspring are given in Table 8.

The hybrid nature of the plants listed in Table 7 (excluding those cited by

Table 7. **Natural hybrids of Heliconia involving species with pendent inflorescences.**

Hybrid combination	Country	Voucher number* or literature citation
H. curtispatha × **H. pogonantha**	Panama	*Kress 80-1144, 80-1156*
H. mariae × **H. pogonantha**	Costa Rica	*Kress 76-627, 76-659, 77-795, 77-875* *Williams 686*
H. nutans × **H. lankesteri**	Panama	*Kress & Clarkson 79-1089c*
H. secunda × **H. clinophila**	Costa Rica	*Kress 77-777*
H. stilesii × **H. danielsiana**	Costa Rica	Daniels & Stiles (1979)
H. tortuosa × **H. nutans**	Costa Rica	Daniels & Stiles (1979)

*For collection localities and herbaria, see "Specimens Examined" under each hybrid in text.

TABLE 8. **Morphological comparison of Heliconia curtispatha, H. pogonantha var. holerythra, H. mariae, and their putative hybrids.**

CHARACTER	H. CURTISPATHA	"HYBRID"	H. POGONANTHA VAR. HOLERYTHRA	"HYBRID"	H. MARIAE
Height (m)	6–7	7–8	4.5–7.5	6	4–7.5
Petiole					
Length (m)	0.9–1.5	1.7–2	1.1–1.8	1.2–1.4	0.9–1.7
Diameter (cm)	1.5–2.3	2.2	2–3	2.2–2.6	1.5–2.5
Leafblade					
Lower surface	Glaucous	Glaucous	Slightly glaucous	Glabrous	Glabrous
Length (m)	1.9–2.3	2.8–3	2–3.3	2.3–2.7	1.7–2.5
Width (cm)	35–55	50–60	40–65	50–60	45–65
Peduncle vestiture	Absent to scurfy	Scurfy	Scurfy	Scurfy	Densely scurfy
Inflorescence length (excluding peduncle) (m)	1.6	1.5	1.6	1	0.65
Rachis					
Vestiture	Puberulous to scurfy	Puberulous to scurfy	Scurfy	Scurfy	Absent to scurfy
Diameter (cm)	1.2–1.8	2	2–2.5	1.8–2.2	1.5–1.8
Cincinnal bracts					
Arrangement	Distichous to spiral	Spiral	Spiral	Distichous to spiral	Distichous
Orientation (to inflorescence axis)	35–50°	50–60°	40–60°	40–50°	80–90°
Inner surface color	Yellow-orange to pink	Yellow to red	Yellow-red	White to yellow to pink	White to pink
Inner surface vestiture	Tomentose to velutinous	Puberulous to pubescent	Puberulous	Absent to puberulous	Absent
Outer surface color	Red to yellow-orange	Rose-red	Red	Red	Pink to red
Outer surface vestiture	Puberulous	Absent	Puberulous	Puberulous to scurfy	Absent to scurfy

Length (cm)	8.5–11.5	12–15	10–13	6–11	4.5–6.5
Width (cm)	6.5–9	7–9	11–16	8–12	7.5–9
Floral bract vestiture (abaxially)	Velutinous to villous	Pubescent	Absent to velutinous	Absent to villous	Absent to puberulous
Pedicel					
Color	White to yellow	White to pink	White to pink	White	White to pink
Vestiture	Absent to puberulous	Absent to puberulous	Absent	Absent to puberulous	Absent to puberulous
Perianth					
Color (base/apex)	White to yellow/deep yellow	Pink/yellow	White to pink/yellow	White/yellow suffused with pink	White/pink to red
Vestiture	Absent, to slightly puberulous apically	Absent to puberulous	Absent basally, velutinous apically	Absent basally, pubescent apically and along sepal margins	Absent basally, puberulous apically
Length (cm)	5.5–6.5	4.6–6	5–5.7	4–5	3–4
Curvature, shape	70–90°, parabolic	90°, parabolic	75–85°, sigmoid	70°, parabolic	50–70°, parabolic
Staminode					
Color	White	White	White, yellow at apex	White, yellow at apex	White
Apex	Cuspidate	Cuspidate	Acuminate	Acuminate	Acute to acuminate
Length (mm)	6–8	7	6–8	5–6	5–7
Drupe					
Length (cm)	1.7	(no fruits seen)	1.5–2	1.3–1.5	1–1.2
Width (cm)	1	(no fruits seen)	1–1.3	0.9–1	0.7–0.9
Flowering	Throughout year	January to August	January to August	(January? to) August	Throughout year
Habitat	Old secondary and primary forest	Open secondary growth	Open secondary growth	Open secondary growth	Open secondary growth

Daniels and Stiles, 1979) was evaluated according to several criteria. In all cases the hybrid individual was intermediate in many of the parental morphological characters (see TABLE 8) and was easily distinguished in the field from both parents, which were always growing in the immediate vicinity. Except for *Heliconia nutans* × *H. lankesteri,* hybrids were usually found in areas of recent disturbance, indicating possible breakdown of habitat- and pollinator-isolating mechanisms. Hybrid pollen grains appeared distorted and highly variable in size under the scanning electron microscope (Kress & Stone, 1983), and they germinated poorly in sucrose solutions. Natural hybrids of *Heliconia* rarely produce viable seed (Stiles, 1979; pers. obs.). However, in the most common hybrid, *H. mariae* × *H. pogonantha,* mature fruits containing fully formed seeds have been found. In no case, except possibly in *H. nutans* × *H. lankesteri,* was any type of "hybrid swarm" apparent; all hybrids occurred as a single individual plant.

Heliconia curtispatha Peterson × **H. pogonantha** var. **holerythra** Daniels & Stiles

SPECIMENS EXAMINED. **Panama.** COLÓN: along Río Guanche, elev. ca. 100 ft, *Kress et al. 80-1156* (DUKE). PANAMÁ: El Llano–Cartí Rd., 15 km from Pan Am Hwy. turnoff, elev. 1200 ft, *Kress & Hammel 80-1144* (DUKE).

Heliconia mariae J. D. Hooker × **H. pogonantha** var. **holerythra** Daniels & Stiles

SPECIMENS EXAMINED. **Costa Rica.** LIMÓN: along road between Puerto Viejo and BriBrí, elev. ca. 100 m, *Kress et al. 76-627* (DUKE), *Kress 77-795* (DUKE). **Panama.** COLÓN: along Río Guanche, elev. 25 m, *Kress 76-659* (DUKE); along roadside near Río Buenaventura, 3 mi from Portobelo, ca. sea level, *Kress 77-875* (DUKE). DARIÉN: Marraganti and vic., elev. 10–200 ft, *Williams 686* (NY).

Heliconia nutans Woodson × **H. lankesteri** var. **rubra** Daniels & Stiles

SPECIMEN EXAMINED. **Panama.** CHIRIQUÍ: in forest along Río Chiriquí Viejo below Cerro Punta, elev. 5500 ft, *Kress & Clarkson 79-1089c* (DUKE).

Heliconia secunda R. R. Smith var. **secunda** × **H. clinophila** R. R. Smith

SPECIMEN EXAMINED. **Costa Rica.** HEREDIA: near waterfall at Cinchona, elev. 4400 ft, *Kress 77-777* (DUKE).

Heliconia stilesii Kress × **H. danielsiana** Kress

Reported by Daniels and Stiles (1979) to occur around Golfito, Puntarenas, Costa Rica. No specimens cited.

Heliconia tortuosa Griggs × **H. nutans** Woodson

Reported by Daniels and Stiles (1979) to occur at Las Alturas, Puntarenas, Costa Rica. No specimens cited.

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EXPLANATION OF PLATES

PLATE I

Three species of the *trichocarpa* group. A, B, *Heliconia necrobracteata*: A, inflorescence, × 0.2; B, flower, × 1. C, D, *H. maculata*: C, inflorescence, × 0.14; D, flower, × 0.8. E, F, *H. talamancana*: E, inflorescence, × 0.1; F, flower, × 0.8.

PLATE II

Two species of the *trichocarpa* group. A, C, *Heliconia colgantea*: A, inflorescence, × 0.1; C, flower, × 1. B, D, *H. trichocarpa*: B, inflorescence, × 0.1; D, flower, × 1.

PLATE III

Three species of the *nutans* group. A, B, *Heliconia marginata*: A, inflorescence, × 0.25; B, flower, × 0.75. C, D, *H. secunda*: C, inflorescence, × 0.18; D, flower, × 0.75. E, F, *H. nutans*: E, inflorescence, × 0.25; F, flower, × 1.

PLATE IV

Two species of the *nutans* group. A, C, *Heliconia platystachys*: A, inflorescence, × 0.08; C, flower, × 1.5. B, D, *H. collinsiana* var. *collinsiana*: B, inflorescence, × 0.14; D, flower, × 1.

PLATE V

Species of the *curtispatha* group. A, C, *Heliconia curtispatha*: A, inflorescence, × 0.1; C, flower, × 0.9. B, D, *H. stilesii*: B, inflorescence, × 0.18; D, flower, × 0.8.

PLATE VI

Two species of the *pogonantha* group. A, C, *Heliconia sessilis*: A, inflorescence, × 0.13; C, flower, × 1.5. B, D, *H. mariae*: B, inflorescence, × 0.18; D, flower, × 1.5.

PLATE VII

Two species of the *pogonantha* group. A, C, *Heliconia pogonantha* var. *veraguasensis*: A, inflorescence, × 0.08; C, flower, × 0.75. B, D, *H. ramonensis* var. *lanuginosa*: B, inflorescence, × 0.1; D, flower, × 1.

PLATE VIII

Three species of the *pogonantha* group. A, D, *Heliconia danielsiana*: A, inflorescence, × 0.1; D, flower, × 0.8. B, E, *H. magnifica*: B, inflorescence, × 0.1; E, flower, × 0.8. C, F, *H. xanthovillosa*: C, inflorescence, × 0.1; F, flower, × 0.75.

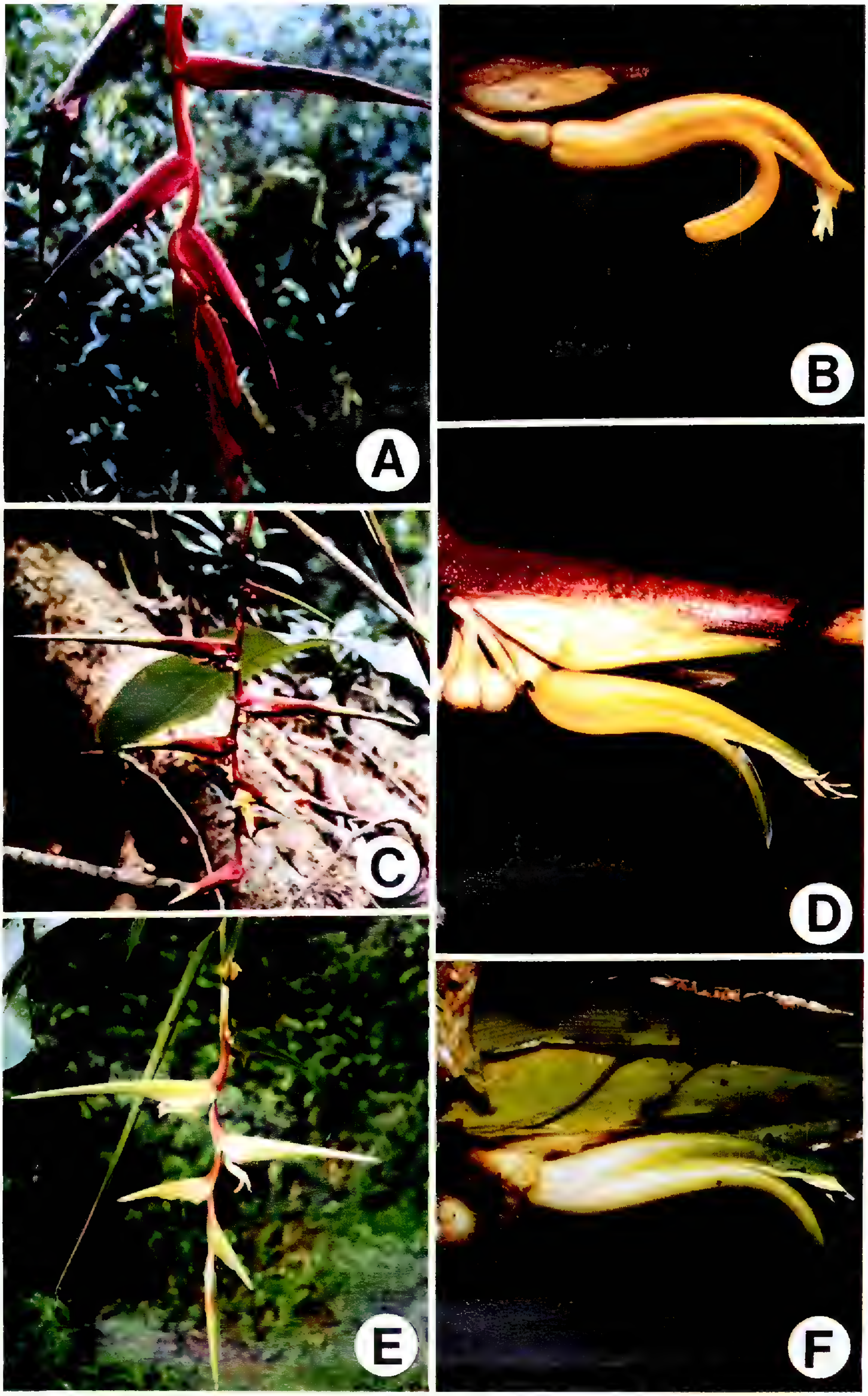
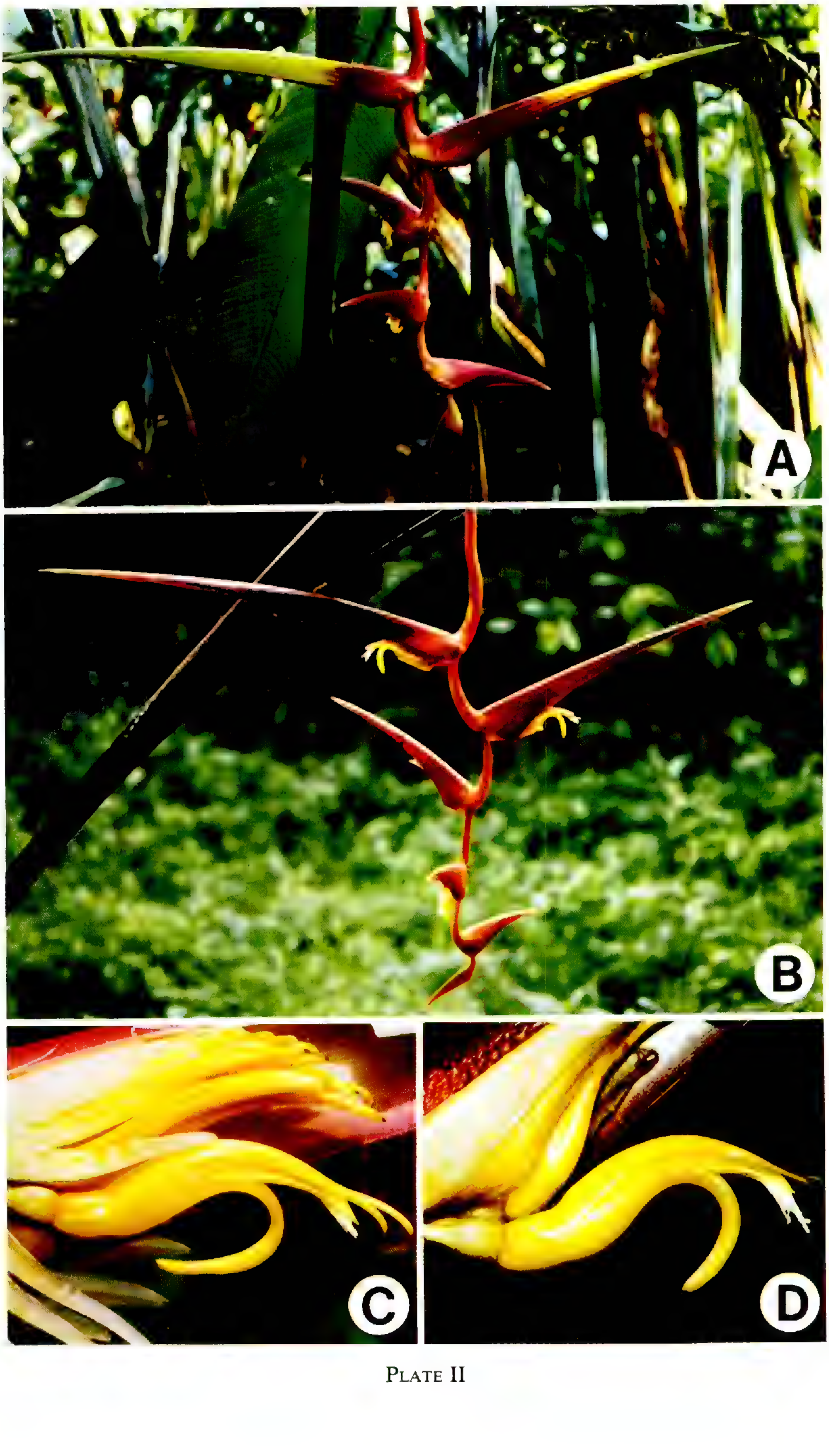


PLATE I



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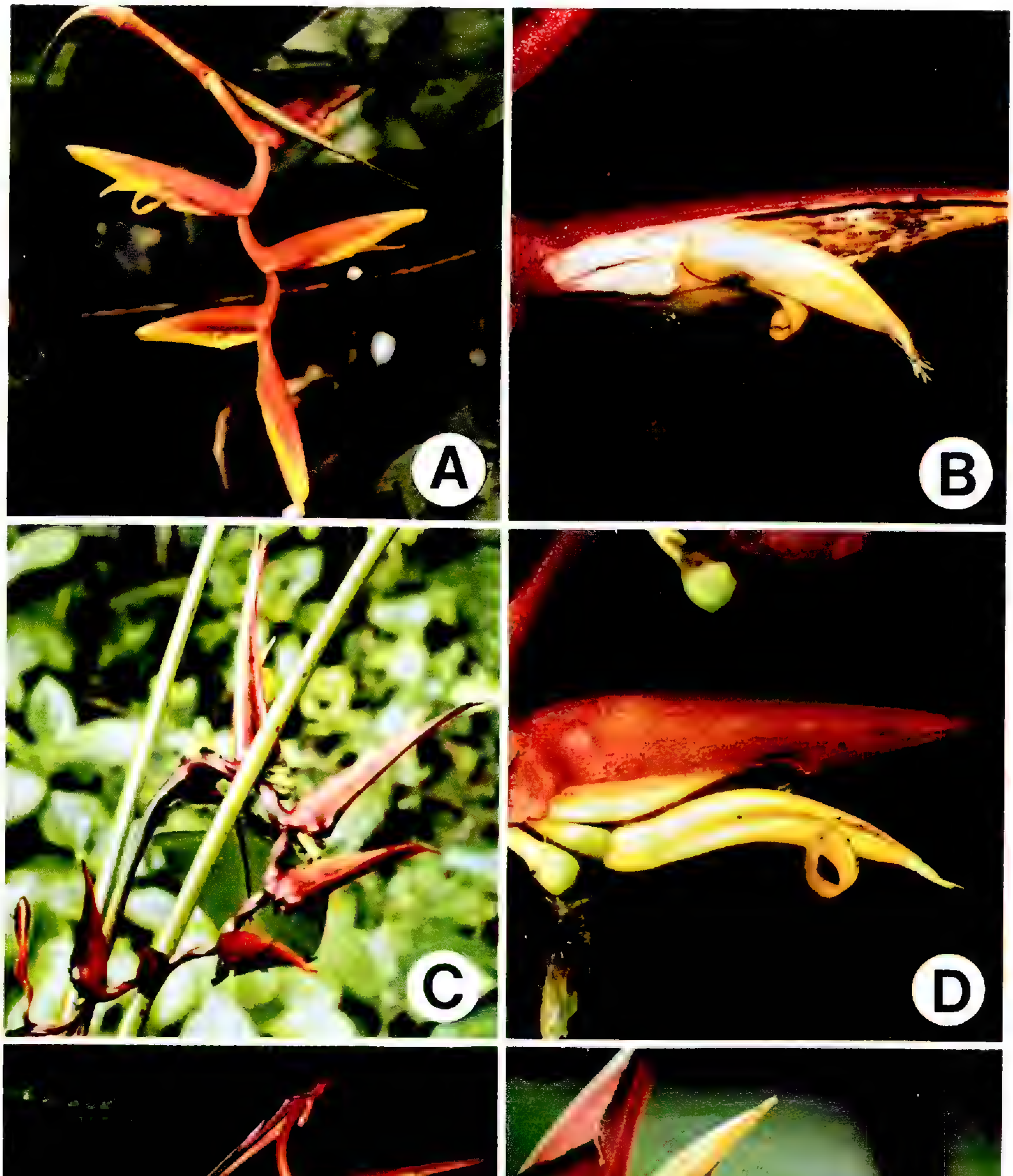

PLATE III

PLATE IV

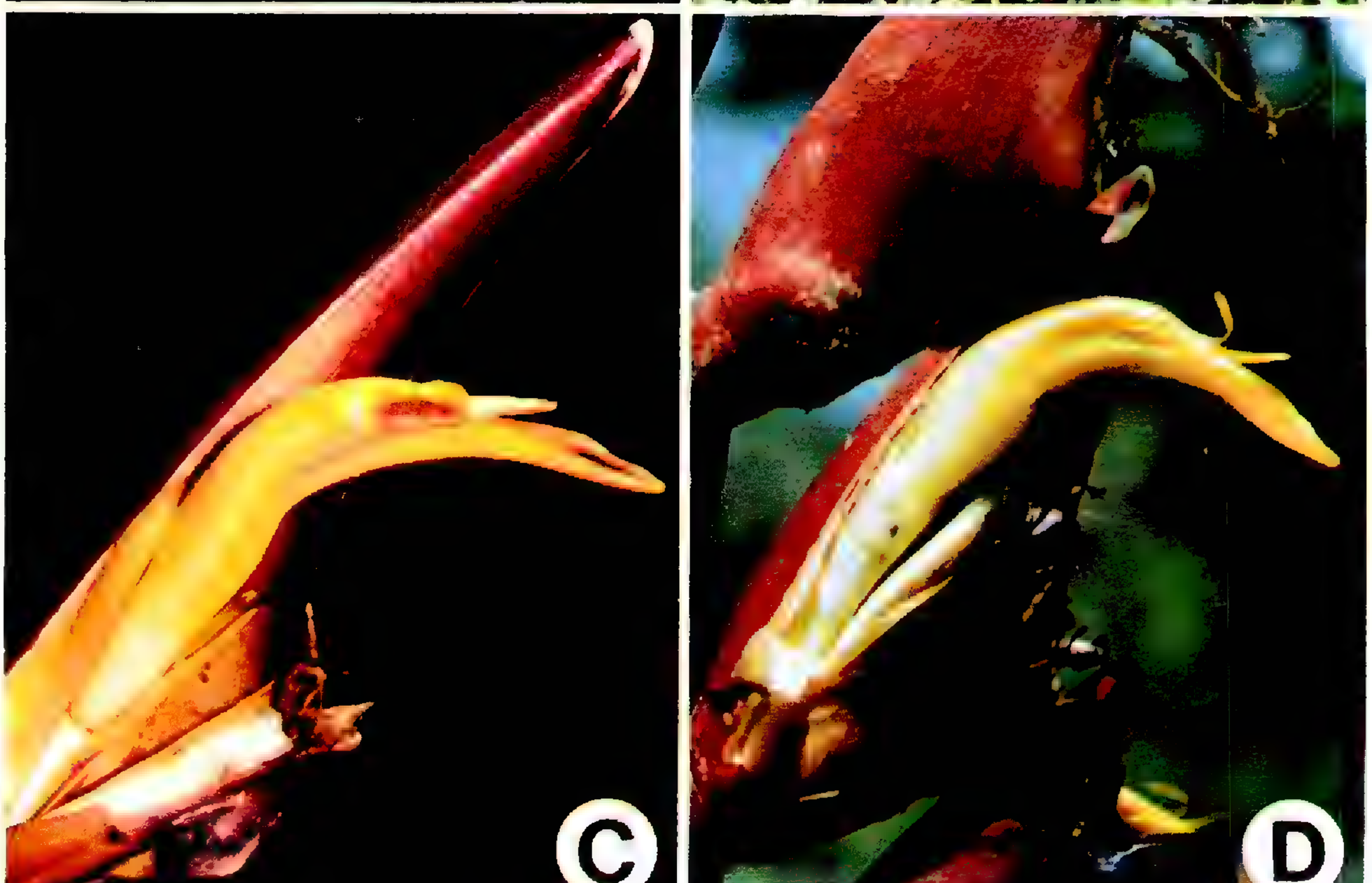

PLATE V

PLATE VI

PLATE VII

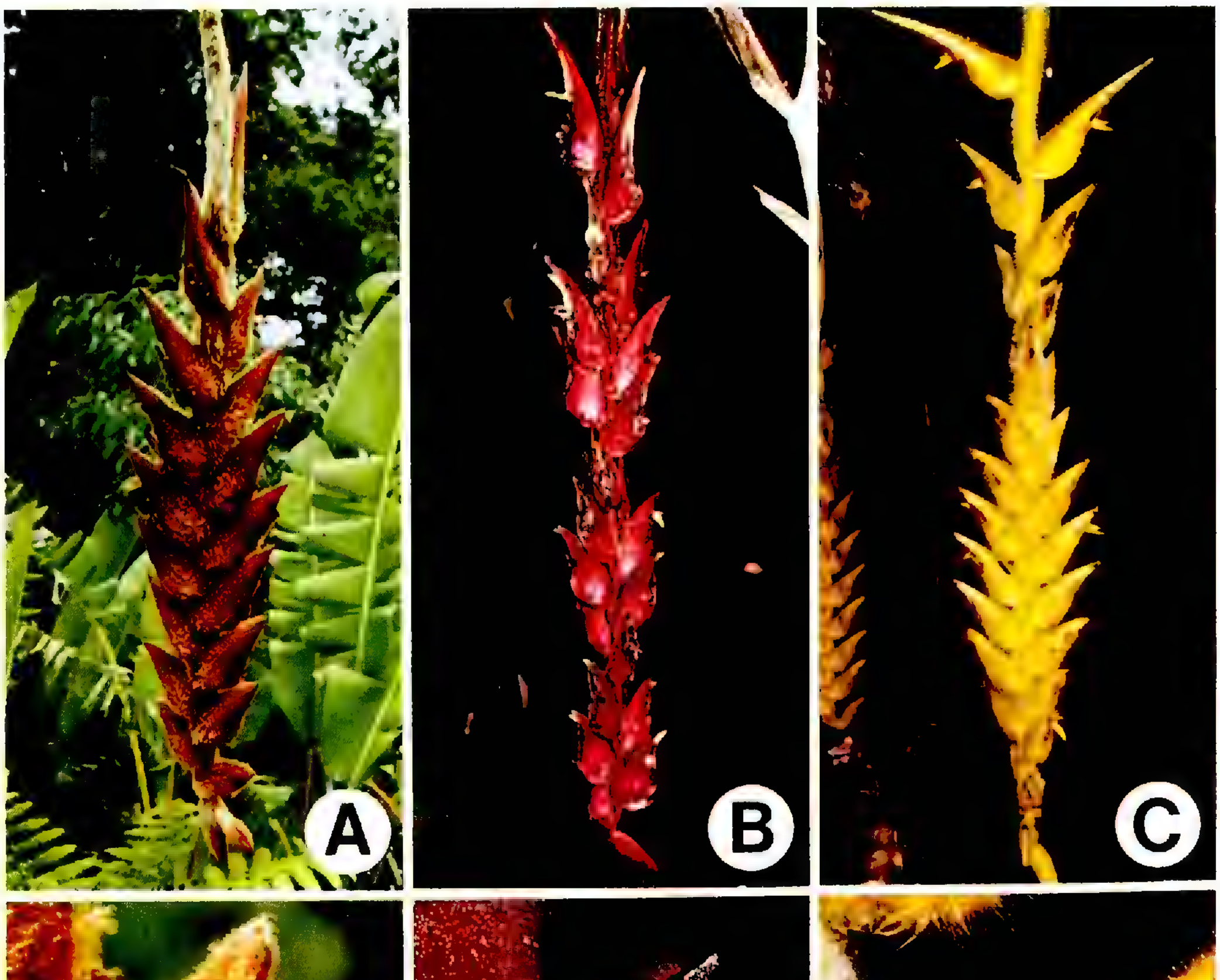

PLATE VIII

THE PLANTAGINACEAE IN THE SOUTHEASTERN UNITED STATES[1]

THOMAS J. ROSATTI

PLANTAGINACEAE A. L. de Jussieu, Gen. Pl. 89. 1789, "Plantagines," nom. cons.

(PLANTAIN FAMILY)

A small family of terrestrial [to aquatic], mostly acaulescent herbs [or occasionally woody subshrubs] with simple, usually alternate, exstipulate leaves. Flowers mostly perfect, small, inconspicuous, usually numerous in cylindrical [to capitate] axillary spikes, mostly proterogynous and wind pollinated. Perianth for the most part actinomorphic and membranaceous-scarious. Sepals 4 [rarely 3], imbricate, the margins glabrous to [rarely long-]ciliate. Corolla salverform [or rarely the lobes indistinct] with 4 (sometimes 2) [rarely 1] stamens alternate with the petals, anthers versatile, filaments long and adnate to the tube. Gynoecium of 2 completely connate carpels, the style filiform, the ovary

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The illustration was prepared by Karen Stoutsenberger, under the direction of Carroll Wood and Kenneth R. Robertson, from fresh or preserved material collected by Wood and/or Robertson in Massachusetts and by Robertson and Ray E. Umber in North Carolina.

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superior, 2- [rarely 1-]locular, with 1 to many anatropous to hemianatropous ovules per locule and axile [or basal or subbasal] placentation. Fruit a circumscissile [or rarely indehiscent] capsule [or stony achene]. Seed with a longitudinally [rarely transversely] oriented embryo in fleshy endosperm, the seed coat more or less mucilaginous when wet. (Including Littorellaceae S. F. Gray; Psylliaceae Horaninow, nomen superfluum.) TYPE GENUS: *Plantago* L.

Three genera and 220–275 species; represented in the southeastern United States by 12 (or perhaps 13) species of *Plantago,* a widely distributed and polytypic genus. *Plantago* differs from *Bougueria* Dcne. and *Littorella* Berg. in its axile (vs. basal or subbasal) placentation, its two-locular (vs. one-locular) ovary, and its two- to many-seeded (rarely one-seeded), circumscissile capsule (vs. stony achene). Barnéoud divided the family into two tribes, primarily on the basis of these differences in fruit.

The three species of *Littorella* (*L. uniflora* (L.) Ascherson, $2n = 24$, of western and central Europe; *L. americana* Fern., $2n = 24$, of northeastern North America; and *L. australis* Griseb. ex Bentham & Hooker, of Chile and Argentina) occur on the shores of lakes and ponds and the margins of quiet streams. They are monoecious herbs with spicate inflorescences in which two carpellate flowers are nearly at ground level and are separated from a single, subterminal flower. (In *L. australis* the carpellate and staminate flowers may be more numerous and less separated.) The carpellate flowers develop one essentially sessile ovule, and at maturity the embryo is parallel to the long axis of the seed. In the single, slightly woody species of *Bougueria* (*B. nubicola* Dcne., $2n = 12$), a poorly collected plant of the high Andes in Peru, Bolivia, and Argentina, the inflorescence is a congested capitate spike in which perfect flowers are lower and more numerous than carpellate ones (although opinion varies on this point). The solitary ovules of both types of flowers are stalked, and at maturity the embryo is perpendicular to the long axis of the seed.

The various proposed affinities of the Plantaginaceae have been much disputed, although several authors have suggested an alliance with the Plumbaginaceae and/or Primulaceae, and in more recent years a relationship with the Scrophulariaceae has attained a certain level of acceptance.

Endlicher united the Plantaginaceae and the Plumbaginaceae in his "Plumbagines" despite the fact that members of the Plumbaginaceae have five-merous flowers, stamens opposite the petals, and seeds with a mealy endosperm. Decaisne compared the Plantaginaceae with the Primulaceae, some members of which have circumscissile capsules, and Bentham and Hooker placed them near the end of their "Gamopetalae," calling it an anomalous family reminiscent of the endospermous Acanthaceae in seed structure and insertion. The family was positioned between the Phrymaceae and the Rubiaceae in *Die natürlichen Pflanzenfamilien* (see Harms & Reiche), and Bessey included it with the Primulaceae and the Plumbaginaceae in his Primulales. Hutchinson (1959) put the family in a monotypic order immediately after the Plumbaginaceae (Primulales) and before the Crassulaceae (Saxifragales). Melchior positioned an identically circumscribed Plantaginales between the Solanales and the Dipsacales (and the family between the Phrymaceae and Caprifoliaceae).

Airy Shaw (in Willis) proposed that the Plantaginaceae are allied with the Scrophulariaceae, stating that the "flower is usually regarded as derived from a five-merous type in the same way [i.e., by suppression of one calyx lobe and complete fusion of two corolla lobes] as that of *Veronica* (Scrophulariaceae), and there are good grounds (including entomological, *viz.* the food-plants of certain Lepidoptera and Coleoptera) for believing that the Plantaginaceae are in fact allied to Scrophulariaceae." Most subsequent authors have conceded such a relationship. Thorne (1976) placed the family in his Bignoniales (with six other families) between the Scrophulariaceae and the Lentibulariaceae. Dahlgren included it in the Scrophulariales (composed of Thorne's Bignoniales and ten other families). Takhtajan put it in the suborder Scrophulariineae between the Gesneriaceae and the Lentibulariaceae and stated that the Plantaginaceae are "near to and derived from Scrophulariaceae." Cronquist (1981) more or less agreed with such an ancestry, but he nevertheless maintained the Plantaginales as a distinct order. (Although Cronquist earlier [1968] had noted that without anemophily and the persistent, scarious corolla, the Plantaginaceae could be positioned in the Polemoniales, he also pointed out that the occurrence in the family of both micropylar and chalazal haustoria was in agreement with a relationship to the Scrophulariaceae.)

Numerous studies have indicated that the Plantaginaceae are rather homogeneous chemically. Hegnauer discovered that species of both *Plantago* and *Littorella* produce aucubin (an iridoid glucoside; Jensen *et al.* indicated a common origin for all iridoid-containing taxa), and Bourdu *et al.* showed that species of these two genera store the same saccharides (stachyose being the most abundant) in comparable proportions in the roots and stems. The seeds of *L. uniflora* contain planteose and saccharose; those of *Plantago* have planteose but in some species stachyose as well (Bourdu *et al.*, Bourdu & Gorenflot). Wallaart identified sorbitol (a sugar alcohol) from the leaves of *L. uniflora* and ten species of *Plantago* and considered the accumulation of this hexitol to be a family character. Aucubin and planteose were also identified in the seeds of eight species of *Plantago* (including *P. major* L.) in Egypt (Ahmed *et al.*).

Chemical evidence has also suggested that the Plantaginaceae are much more closely related to the Scrophulariaceae than to either the Plumbaginaceae or the Primulaceae (Bourdu *et al.*, Gibbs, Hegnauer). Aucubin has been found as well in the Globulariaceae, Loganiaceae, Orobanchaceae, and Scrophulariaceae (Bate-Smith). The production of mannitol (a stereoisomer of sorbitol) by two species of *Plantago* also indicates a strong biochemical link with the Scrophulariaceae, according to Wallaart. The Plumbaginaceae and Primulaceae are among 68 families in which both leuco-anthocyanins and trihydroxy constituents have been identified, while the Scrophulariaceae and Plantaginaceae are among 70 families in which these compounds are not known (Bate-Smith). Seigler reported that while members of the Plumbaginaceae and Primulaceae do not have iridoid monoterpenes, such compounds have been found in about 41 other families, including the Scrophulariaceae and the Plantaginaceae. According to Alston and Turner, both the Scrophulariaceae and the Plantaginaceae are among about 20 families, exclusive of the Plumbaginaceae and the Primulaceae, in which linoleic acid and oleic acid are the major fatty acids.

The most common and widespread (and therefore, presumably, the ancestral) base chromosome number in the Plantaginaceae is six. (The Scrophulariaceae have six among their base numbers, but only the Plumbaginaceae have chromosomes with any morphological similarity to *Plantago* [McCullagh].) Diploids, triploids, tetraploids, hexaploids, octaploids, 12-ploids, and 16-ploids (i.e., $2n = 12$, 18, 24, 36, 48, 72, and 96) are known in *Plantago,* while only diploids and tetraploids (in the same series) have been reported for *Bougueria* (Rahn) and *Littorella,* respectively. The base numbers five (diploids, tetraploids, hexaploids, and decaploids) and four (diploids and tetraploids) have been reported in *Plantago* and are less common in the family. Aneuploids at numerous levels have also been reported in *Plantago* (see primarily Bolkhovskikh *et al.*).

Species of *Plantago* and *Littorella* shed binucleate pollen, except that that of *P. lanceolata* L. is trinucleate (Brewbaker). *Bougueria* is evidently unknown in this regard.

The pollen in the Plantaginaceae (which provides no clear indication of the systematic placement of the family [Erdtman]) is usually spheroidal (but sometimes ovoid or irregular) and more or less distinctly periporate, with the pores circular or irregular in shape. After some initial confusion that appears to have been resolved by the use of scanning electron microscopy, there is now agreement that the sculpturing is more or less verrucate. Although the outermost layer of ornamentation has been alternately described as micro-echinate (Bassett *et al.,* Bassett & Crompton) or scabrate (Clarke & Jones), the latter is the more appropriate term (according to Clarke & Jones) because the projections are rounded. Discrepancies regarding the presence or absence of annuli and opercula also exist in the literature, apparently because of a failure to recognize that within the family a continuum exists between grains possessing and those completely lacking such features (Clarke & Jones).

Because only four species of the Plantaginaceae are in genera other than *Plantago,* studies of topics such as embryology, anatomy, and morphology have mostly involved only species of *Plantago* and are therefore summarized in the generic discussion.

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1. **Plantago** Linnaeus, Sp. Pl. **1:** 112. 1753; Gen. Pl. ed. 5. 52. 1754.

Erect or suberect, acaulescent (but sometimes branched near the base and/or rhizomatous) [or caulescent (and branched)], terrestrial, annual, biennial, or perennial herbs [or occasionally woody subshrubs]. Leaves simple, linear, lanceolate to oblanceolate, spatulate, ovate, or cordate; alternate, in basal rosettes [or, less frequently, alternate or opposite on sparsely to densely branched stems], exstipulate, with dilated, sometimes sheathing bases, glabrous or (rarely) densely pubescent (at least adaxially), entire, dentate, [or pinnatifid], one to many nerved, the blade and petiole distinct or not. Plants with only perfect flowers (or otherwise, usually with perfect and carpellate flowers on separate plants) [rarely dioecious]. Inflorescences axillary with cleistogamous or chasmogamous flowers sparsely to densely organized into long to short, cylindrical [to capitate] spikes. Flowers single in the axils of bracts, small, usually numerous, (chasmogamous flowers) mostly proterogynous and wind pollinated, and actinomorphic or slightly zygomorphic (with respect to corolla lobes). Sepals 4, imbricate, membranaceous-scarious, equal or in 2 unequal pairs (the abaxial pair sometimes connate in the basal half), alternate with the subtending bract, and often keeled [or rarely with many distinct nerves]. Corolla salverform with the tube ovoid to cylindrical and the 4 erect, spreading, or recurved lobes distinct, imbricate, membranaceous-scarious, and alternate with the sepals. Stamens 4 (occasionally 2), adnate to the corolla tube (rarely below the gynoecium), alternate with the petals; filaments filiform, induplicate in bud; anthers included or exserted, cordate, often apiculate, 2-locular, dorsifixed, versatile, and with longitudinal, latrorse to slightly introrse dehiscence. Carpels 2, connate; stigmas included or exserted; style filiform; ovary superior, 2-locular [or imperfectly

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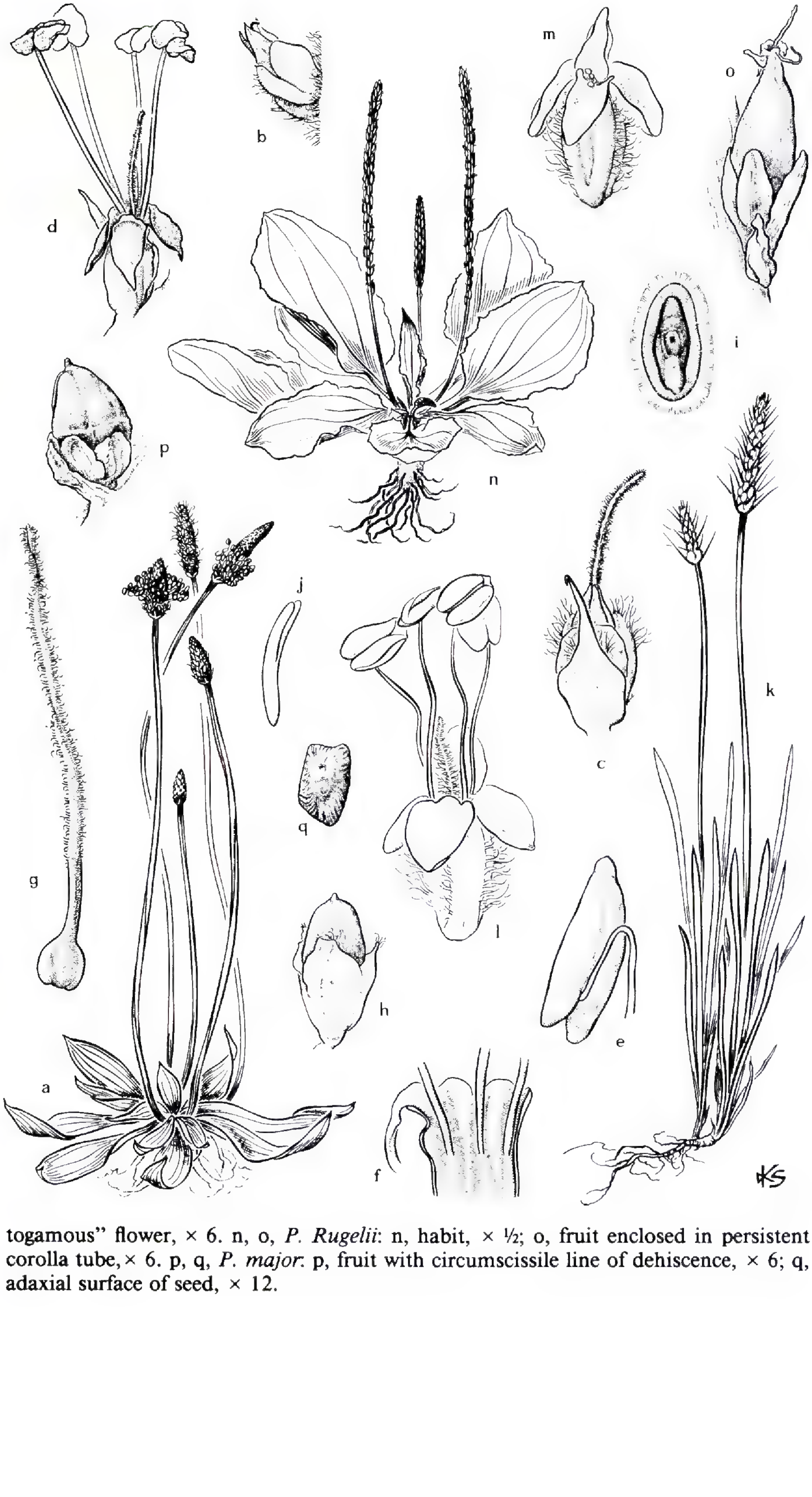
FIGURE 1. **Plantago.** a–j, *P. lanceolata*: a, habit, inflorescences with flowers immature, or with only styles protruding, or at anthesis, × ½; b, flower bud subtended by bract, × 6; c, flower with receptive style protruding, subtending bract in front, × 6; d, flower, later stage with corolla lobes open and anthers dehiscing, × 6; e, versatile anther, × 12; f, portion of corolla tube in section, filament bases inserted between folds of corolla, × 12; g, gynoecium, × 12; h, capsule surrounded by persistent calyx, × 6; i, adaxial surface of moistened seed, outer layer mucilaginous, × 6; j, embryo, × 6. k–m, *P. aristata*: k, habit—note long inflorescence bracts, × ½; l, flower at anthesis, × 6; m, "cleis-



togamous" flower, × 6. n, o, *P. Rugelii*: n, habit, × ½; o, fruit enclosed in persistent corolla tube, × 6. p, q, *P. major*: p, fruit with circumscissile line of dehiscence, × 6; q, adaxial surface of seed, × 12.

3- or 4-locular by the intrusion of false septa from the carpel midrib]. Ovules 1 to many per locule, tenuinucellar, hemianatropous to anatropous, integument single, massive; placentation axile. Fruit a globose to elongate capsule, circumscissile at or below the middle [indehiscent in *P. macrocarpa* Cham. & Schlecht.]; calyx persistent, the corolla usually so (but then irregularly torn about the middle of the tube). Seeds yellow-tan to almost black, often shining, for the most part narrowly elliptic in longitudinal median section (through the widest dimension of the seed); seed coat more or less mucilaginous when wet; endosperm cellular, fleshy; embryo parallel to the long axis of the seed and straight or sometimes curved. (Including *Coronopus* Miller, non Zinn, nom. cons., and *Psyllium* Miller.) LECTOTYPE SPECIES: *P. major* L.; see Britton & Brown, Illus. Fl. No. U.S. & Canada, ed. 2. **3:** 245. 1913. (*Plantago* listed by Linnaeus [Critica Botanica, p. 110. 1737; p. 87 in A. Hort, English transl., 1938] as a Latin name given by the "Ancients" [Pliny and other Roman writers]. According to Clute, and most others who have commented on the issue, the name is from Latin *planta,* signifying the sole of the foot, and *ago,* used in plant names in the sense of "wort" [but also to mean having the characteristics of].)—PLANTAIN.

A nearly cosmopolitan genus occurring largely in the Temperate Zones but only poorly represented in the lowland tropics, *Plantago* is recognized in the most recent worldwide monograph (Pilger) to consist of 258 species. Although perhaps best known for its nearly ubiquitous weedy members (*P. lanceolata* L. and *P. major* L., for example, are extremely widespread and even occur at low elevations in the New World tropics [D'Arcy; Dietrich, 1979]), most species are in fact of much more restricted distribution. Some are endemic to very small areas and/or are highly specialized ecologically. The genus is best represented in the Mediterranean region, the Himalayas, southwestern North America, and the mountains of South America.

Since Linnaeus (Species Plantarum, 1753) grouped the species of *Plantago* into those with *scapo nudo* and those with *caule ramosa,* suprasectional taxa have been recognized in the genus by Barnéoud (1844; two units based on seed number per capsule and seed shape in transverse median section), Harms (in Harms & Reiche; two subgenera based on leaf arrangement), Pilger (two subgenera based on leaf arrangement), and Rahn (1978a; three subgenera based on ovule/seed number per ovary/capsule, seed shape in transverse median section, corolla-tube pubescence, leaf shape, embryo orientation [plane between the cotyledons either parallel, oblique, or perpendicular to the adaxial surface of the seed], and chromosome number). The genus has also been divided into various numbers of sections by Barnéoud (1844), Decaisne, Harms (in Harms & Reiche), Pilger, and Rahn (1978a) based on different combinations of characters including spike morphology (size, shape, and flower arrangement and density), corolla pubescence, corolla-lobe shape, anther and stigma inclusion or exsertion, seed size, seed number per capsule, seed shape (in transverse median section as well as longitudinal median section through the widest dimension of the seed), leaf shape, degree of stem lignification, plant duration, and geographic distribution. Rahn (1978a) recently typified a number of subge-

neric and sectional names in *Plantago,* and his infrageneric classification is followed here.

Approximately 24 indigenous and eight naturalized species of *Plantago* representing all three subgenera and ten of the sections enumerated by Rahn (1978a) occur in North America. Twelve (or perhaps 13) species in two subgenera and six (or perhaps seven) sections grow in the southeastern United States. The first four sections discussed below were placed in subg. PLANTAGO; the last three in subg. PSYLLIUM (Miller) Harms in Harms and Reiche. Ten of our species are indigenous to North America, and four of these appear to be naturalized in the Southeast (i.e., are native to other parts of the continent).

The predominantly Old World sect. PLANTAGO (fibrous-rooted perennials with petiolate leaves, elongate-cylindrical spikes, exserted anthers and stigmas, and 4–20 seeds per capsule) comprises about 19 species, including a closely related pair occurring in the Southeast. *Plantago major,* $2n = 12, 18, 24$, thought to be a native of Europe and northern and central Asia but now established throughout most of the rest of the world, is a weed that reportedly occurs in most parts of our range, although it is poorly collected and/or perhaps rare in our area. *Plantago Rugelii* Dcne., $2n = 24$, originally native to eastern North America, is a weedy species now widely established westward but at best uncommon outside of this continent. (It grows at or near sea level in Cuba [Dietrich, 1979] and has evidently become established in northern Europe [Hansen].) *Plantago Rugelii* occurs throughout the Southeast, but it seems to be poorly represented, if not absent, in peninsular Florida. *Plantago Rugelii* differs from *P. major* in its more elongate capsules that dehisce closer to the base and often contain fewer seeds; otherwise the species are remarkably similar morphologically. Although *P. major* and *P. Rugelii* usually grow (but not necessarily together) in fields, lawns, roadsides, sidewalks, and paths, both Tessene (1968) and Bassett (1973) have reported that *P. major* does not thrive in shaded and/or continually wet places and that *P. Rugelii* may be found in open woods and along damp shorelines. Hamilton and Buchholtz, however, counted significantly fewer seedlings of *P. Rugelii* in shaded plots than in open ones (all plots naturally seeded). *Plantago major* may be particularly well adapted to areas where the soil has been trampled (Blom; Sagar & Harper, 1960; Warwick) or compacted (Blom; see, however, Noe & Blom and Tessene, 1968). Hawthorn and Cavers (1976) found that in natural (pasture) populations, *P. Rugelii* had a longer half-life than *P. major* with regard to both seedlings and mature plants, while individuals of *P. major* flowered in greater numbers (proportionately) and earlier in development. Several authors have reported that *P. major* can be either an annual or a perennial (see Hawthorn & Cavers, 1976).

Four of the six species comprising the Old and New World sect. MICROPSYLLIUM Dcne. (taprooted annuals with linear leaves and loose, elongate spikes bearing small flowers with usually two stamens and included anthers and stigmas) occur in North America (see Bassett, 1966), and the two present in our range, *Plantago heterophylla* Nutt., $2n = 12, 22$, and *P. pusilla* Nutt., $2n = 12$, are nearly indistinguishable. Both have erect corolla lobes, but *P. heterophylla* has many (usually 10–25) small seeds per capsule, while the fruits

of *P. pusilla* almost invariably contain four larger seeds.[2] Very small individuals occur in both species. *Plantago heterophylla* is more common than *P. pusilla* in the Southeast (in North America it is almost restricted to our area). It grows in moist, sandy or silty soils and is frequently a weed in cultivated or waste places. It is an adventive in California (Pilger) and in the northeastern United States (northward to southern New York [Bassett, 1966]), but it is evidently indigenous in Argentina and Paraguay (Pilger). *Plantago pusilla* is most often found in disturbed areas. Its rather limited natural range includes the southern three-fourths of Missouri and adjacent states. *Plantago pusilla* has become established in the East from North Carolina to Massachusetts, and more sporadically in the West between southern California and southwestern Washington (Bassett, 1966). In our area, therefore, it occurs as a native in Arkansas and Tennessee and as an adventive in northeastern North Carolina.

The nearly cosmopolitan and rather poorly distinguished sect. PALAEOPSYLLIUM Pilger (thick-rooted perennials with ovate-cordate to oblanceolate leaves having relatively distinct petioles; loose, elongate spikes bearing large flowers with exserted anthers and stigmas; and two to nine seeds per capsule) consists of about 28 species, of which four are North American (see Bassett, 1967). Two of these occur in the Southeast.

Plantago cordata Lam., $2n = 24$, has distinctly petiolate leaves with ovate to cordate blades and veins that appear to arise from a midrib (vs. from the base of the blade, as in the rest of the genus), hollow scapes, sepals that are about as long as the bracts, and two- to four-seeded capsules that dehisce approximately at the middle. The species is unique in the genus in that the fruits are still green and alive at the time of dehiscence, when the lid of the pyxis readily falls off, and the two or three seeds with the entire fleshy placenta fall out as a unit (Tessene, 1969). This structure is buoyant and may represent an adaptation to dispersal by water. The plants grow in alluvial woods, on wet rocky banks, in streams through areas of slate bedrock, and in the shallow soil of cedar (*Juniperus virginiana*) barrens in our area. The species probably occurs in all of the southeastern states, although it is perhaps absent from southern Florida and is apparently unknown outside of North America. *Plantago cordata* differs from *P. major* and *P. Rugelii,* with which it is often confused, in a number of ways. Its leaves are larger, the blades are more abruptly contracted to the petiole (but not always cordate), and the major veins, although actually parallel, approach a pinnate arrangement. In addition, the roots are thicker and the flowering time is earlier in *P. cordata.*

[2]*Plantago heterophylla* Nutt. (1835; see Foster) has been the most commonly used name for the plants with ten or more seeds per capsule. Godfrey and Wooten used the earlier name *P. hybrida* W. Barton (1818) for this species and incorrectly listed *P. elongata* Nutt. (instead of *P. heterophylla*) in synonymy. The species with four seeds per capsule has been called *P. elongata* Pursh (1814) or *P. pusilla* Nutt. (1818), depending on taxonomic interpretation, the later name being used if our eastern plants are considered to be specifically distinct from more western populations. Unfortunately, seed number is mentioned in none of the four protologues involved, and I have not been able to study the type specimens. To minimize the likelihood of adding confusion, I have chosen to use the most commonly employed names, *P. heterophylla* and *P. pusilla,* although the reader should be aware that the situation is subject to change.

The second species, *Plantago sparsiflora* Michaux, $2n = 24$, has oblanceolate leaf blades that gradually taper to the petiole, scapes that are only sometimes hollow, sepals that are about twice as long as the bracts, and two-seeded capsules that dehisce below the middle. It is known only from the Coastal Plain of northern Florida and the southeastern portions of Georgia and the Carolinas, where it is frequent in wet or dry savannas, roadsides, and ditches.

Tessene (1969) studied in detail many aspects of *Plantago cordata,* which he considered to be the rarest North American species of the genus. He determined that the characteristic venation of the leaf, so frequently used to distinguish the species, usually does not develop until after fruiting has begun, and that depauperate inflorescences often retain solid peduncles. He stated that it usually grows in calcareous substrates and reported only one instance in which the species was found in a disturbed, man-made habitat (an unshaded drainage ditch). Tessene also attempted crosses between *P. cordata* and eight other species in four sections of *Plantago,* with only one F_1 plant resulting. This hybrid, *P. cordata* × *P. eriopoda* Torrey (both of sect. PALAEOPSYLLIUM) was sterile and intermediate in most characters.

The New World sect. VIRGINICA Barn. (leaves elliptic to spatulate, often dentate; scapes long and with a terminal, many-flowered, cylindrical spike; abaxial sepals much narrower than the adaxial ones; corolla tubes glabrous and lobes erect or spreading; capsules with up to four but usually two or three seeds) was the subject of an ambitious revision based primarily on the morphology of herbarium specimens but influenced by ecological data, cultivation experiments, chromosome studies, hybridizations, and taximetric analyses (Rahn, 1974). Included were sections OREOPHYTUM Dcne., CLEIOSANTHA Dcne., and NOVORBIS Dcne., in addition to species from sections PALAEOPSYLLIUM and LEUCOPSYLLIUM Dcne. Twenty-eight species (four described as new) were recognized in the section (morphologically indistinguishable entities differing in chromosome number were treated as conspecific); five of these occur in North America, and two are found in the Southeast. Both have concave adaxial seed surfaces (vs. plane in the three other species) and are annuals with slender primary roots, pilose leaves, spreading hairs on the scape, erect corolla lobes, and two-seeded capsules.

Plantago virginica L., $2n = 12, 24$ (or ca. 24 [Rahn, 1974]), occurs throughout the eastern half of the United States, including all of the Southeast, and is apparently a waif in southern Ontario (Bassett, 1973). It is more sporadically distributed in the western states and northeastern Mexico. The species appears to be a spring ephemeral (Rahn, 1974; all but four of the 111 specimens I examined were collected earlier than June) and is generally found in dry, sandy soils of waste places, fallow and cultivated fields, and roadsides. *Plantago virginica* can be distinguished from the other common plantagos in our area by its dentate, spatulate leaves, its rather dense, cylindrical spikes, and its persistent corollas with conspicuous, yellow, erect lobes. Depauperate forms of the species are fairly common.

Plantago rhodosperma Dcne., $2n = 24$, occurs in rocky or sandy soils mainly in the southwestern United States and adjacent Mexico. Although Rahn (1974) cited no specimens from our range (and I have seen none), his distribution

map for the species includes Louisiana, most of Arkansas and Mississippi, and southwestern Tennessee. Several other authors (Correll; Small, 1913; Smith; Steyermark) have reported the species from various combinations of these states. *Plantago rhodosperma* differs from *P. virginica* in having acuminate to mucronate (vs. obtuse) abaxial sepals, and broad (vs. narrow) seeds with shallowly (vs. deeply) concave adaxial sides.

The Old World sect. LANCIFOLIA Barn. (sect. *Arnoglossum* Dcne.) (oblanceolate leaves, grooved peduncles, dense spikes, and abaxial sepals fused for more than half their length) consists of perhaps six species, one of which is represented in our area. *Plantago lanceolata,* $2n = 12$, 13, 24, 96, native to Europe and northern and central Asia, is established throughout most of the world, especially in temperate regions. It is an extremely variable species that is widely distributed across temperate North America (except the prairie provinces of Canada) and Mexico in most kinds of disturbed habitats. Perhaps the best-known member of the genus, *P. lanceolata* has been an extremely popular subject for research, some of which is summarized below. (See also Cavers *et al.* for a synthesis of much of the recent information concerning many aspects of its biology.)

Plantago sect. GNAPHALOIDES Barn. (flowers paired or in threes; hairs of the scape wider than those of the leaves, and at least some hairs ascending) comprises the American species included by Pilger in sect. LEUCOPSYLLIUM and was divided into four series by Rahn (1978a). The seven North American species, all $2n = 20$, are in series *Gnaphaloides* Rahn (annuals with well-developed taproots; linear leaves [but wider than those of species in sect. MICROPSYLLIUM]; spikes dense, cylindrical; bracts, especially of the lowermost flowers, often with an elongated green nerve; corolla lobes relatively conspicuous and recurved, with cordate to obtuse bases; and anthers small). Five species, including the three that occur in our range, have zygomorphic corollas with cordate lobes (vs. actinomorphic with slightly cordate or obtuse lobes in the two other species). Of our species, *P. aristata* Michaux and *P. Wrightiana* Dcne. (*P. Hookeriana* Fischer & Meyer var. *nuda* (Gray) Poe) are more common and have adaxial leaf surfaces that are glabrous or nearly so; in the less common *P. patagonica* Jacq. (*P. Purshii* Roemer & Schultes) these surfaces are densely hairy.

Plantago aristata is easily recognized by its conspicuous, often leaflike bracts that are usually smaller toward the apex of the spike. Taxonomically insignificant depauperate individuals with very narrow leaves, reduced flowers, and hairy, few-flowered spikes can be found, but such inflorescences occur on otherwise normal plants, and all intermediate forms exist. *Plantago aristata* is a common weed throughout the eastern United States (with the exception of the extreme north). It grows most commonly in dry, sandy soil along roadsides and in pastures, fields, and other kinds of recently disturbed habitats. It is an adventive in Oregon and California and in various parts of the Old World (Rahn, 1978b). *Plantago Wrightiana* differs most obviously from *P. aristata* in having shorter (and therefore less conspicuous) bracts. According to Rahn (1978b), the species occurs in three disjunct areas: central Arizona; Oklahoma, Texas, and adjacent parts of Mexico; and parts of Mississippi, Alabama, Geor-

gia, Florida, and the Carolinas. (I have, however, seen herbarium specimens from Louisiana and southwestern Arkansas that cast doubt on Rahn's contention that the southeastern populations are disjunct from those in Texas and Oklahoma.) Rahn also stated that, on the basis of ecological data, *P. Wrightiana* is probably not native to our area.

The third of our species in series *Gnaphaloides, Plantago patagonica,* is intermediate in bract width and length between *P. aristata* and *P. Wrightiana.* It is at least an adventive in the Southeast. I have seen three specimens of *P. patagonica* (two were annotated by Rahn in 1975): one from railroad tracks in Cleveland Co., Arkansas, and two specimens from a roadside in Lancaster Co., North Carolina. (Smith has also reported it from Arkansas.) The species is otherwise known from southern and central Argentina; from an area between northern Baja California and south-central British Columbia eastward to the western Great Lakes and central Texas; and from two localities in interior New England (Rahn, 1978b).

Species of sect. PSYLLIUM (Miller) Lam. & DC. (branched, caulescent herbs or subshrubs with opposite or rarely whorled leaves) are native to the Mediterranean region and the Middle East. *Plantago Psyllium* L.,[3] $2n = 12$, an annual with dense, subcapitate spikes and a taproot, has been reported from various parts of the world. In North America it has been collected in sandy and/or waste places. *Plantago Psyllium* is rare in southern Canada (Bassett, 1973), occasional in the northwestern United States (Hitchcock & Cronquist), known from many parts of California because it is often a constituent of commercial bird-seed (Munz), and well established in the eastern United States (Gleason & Cronquist). It is rare and perhaps not persistent in our area. Although it has been reported from coastal dunes in North Carolina (New Hanover Co.; Radford *et al.*), I have seen neither a voucher specimen for this station nor any other specimen from the Southeast.

Cytological studies have provided data that bear, either alone or in combination with palynological information, on various systematic problems in the genus. McCullagh, who studied mitosis in the root tips of 40 species of *Plantago* (including *P. major, P. lanceolata, P. patagonica,* and *P. Psyllium* and allied species), recognized six morphological types of chromosomes. McCullagh concluded that the genus is monophyletic (with new species having arisen by polyploidy, reduction in the number of chromosomes, and hybridization—the latter two processes often followed by chromosomal duplication), and that differences in chromosome morphology do not correlate with the two subgenera based on leaf arrangement (cf. Harms in Harms & Reiche; Pilger). The Old World and American species included by Pilger in sect. LEUCOPSYLLIUM were

[3] There has been some confusion about the nomenclature of this species. Linnaeus (Species Plantarum, 1753, p. 115) described *P. Psyllium* with the phrase "caule ramoso, foliis integerrimis, spicis foliosis," but later (Systema Naturae, 1759, p. 896) used the description "caule ramoso suffruticoso, foliis integerrimis, spicis aphyllis" for *P. Psyllium* and "caule ramoso herbaceo, fol. integerrimis, spicis foliosis" for a new species, *P. indica.* Panigrahi has treated *P. indica* L. (1759) as an illegitimate synonym of *P. Psyllium* L. (1753), and that name in turn as a nomen confusum. The name *P. arenaria* Waldst. & Kit. has been used by Shear and by Chater and Cartier (in Moore, 1976), who listed (in synonymy) *P. Psyllium* as a nomen ambiguum and *P. indica* as a nomen illegitimum.

considered by Rahn (1978a) to form morphologically distinct groups and were therefore placed by him in sections ALBICANS Barn. and GNAPHALOIDES, respectively. This position was reinforced by Bassett and Crompton, who observed that *P. fastigiata* E. L. Morris (*P. insularis* Eastw.) differs from the other North American species of sect. LEUCOPSYLLIUM (i.e., those included in sect. GNAPHALOIDES by Rahn) in several ways, including chromosome number ($2n = 8$ vs. 20) and pollen morphology (for example, smaller grains with operculate pores). Thus, although sections ALBICANS and GNAPHALOIDES appear to be taxonomically distinct, the former is not confined to the Old World and is therefore not geographically isolated from the latter, as was implied by Rahn (1978b). Finally, although both Wodehouse and Bassett (1973) have remarked that *P. major* and *P. Rugelii* differ more palynologically than morphologically, such differences could be due to chromosome number alone: the grains of *P. Rugelii,* a tetraploid, are larger and have more numerous pores than those of *P. major,* primarily a diploid.

An interesting anatomical feature of *Plantago* is the occurrence of cambiform tissue in the cortex and/or pith of the fleshy rhizomes of many species, particularly those in sect. PLANTAGO (Metcalfe & Chalk). These rows of cells appear to represent incompletely developed vascular bundles and are apparently connected with one another (but not with the bundles of the vascular ring). In *P. major* and *P. media* L. they become converted into true medullary vascular bundles.

The tendency for insular members of a group to be more woody than their continental relatives is exemplified by species of *Plantago* (Carlquist). The ability to accumulate secondary xylem has evolved independently in this genus several times, apparently in response to the relative uniformity of island climates. The adaptation of these same species to wetter conditions following migration from drier continental areas has involved an increase in vessel element length and diameter. In *Plantago,* as in other groups of predominantly herbaceous dicots, wood produced by insular species is largely rayless.

Nodal anatomy in *Plantago* is extremely variable and a poor indicator of infrageneric relationships (Misra, 1966). Species in such dissimilar groups as sections CORONOPUS (Miller) Lam. & DC. (of subg. CORONOPUS (Miller) Rahn) and PSYLLIUM (of subg. PSYLLIUM) are unilacunar, while *P. ovata* Forskål (sect. ALBICANS of subg. PSYLLIUM) is trilacunar and *P. Lagopus* L. (sect. LANCIFOLIA of subg. PSYLLIUM) and *P. major* (sect. PLANTAGO) are multilacunar. Anatomical complexity at the nodes appears to be a function of leaf size because unilacunar nodes are found in species with narrow leaves and bases and multilacunar types are associated with broad leaves and sheathing bases.

The presence of an endodermis with Casparian thickenings has been noted in both stems (Metcalfe & Chalk) and leaves (Trapp) in species of *Plantago.* Trapp found that in each of eight examined species (including *P. lanceolata* and *P. major*), the leaf endodermis is structurally no different than that found in angiosperm roots, and experiments showed that it is even potentially capable of arresting the outward diffusion of solutes. He considered it improbable, however, that such a function is actually realized and concluded that the pres-

ence of a foliar endodermis in these plants appears to be neither beneficial nor detrimental to a leaf's functioning.

Leaves of *Plantago* often resemble those of monocotyledons in their narrowness, parallel venation, and sheathing bases. Even species with distinct petioles and blades are often said to be pseudo-laminate, the blade representing (as in monocots) an "expansion of the apical region of the original phyllode" (Arber, 1918). Furthermore, leaf development involves the cessation of intercalary activity and the subsequent maturation of tissues in a basipetal direction, as is well expressed in monocots but is also seen in conifers and other dicots with narrow leaves (Esau).

The stomata of young leaves of *Plantago* are anomocytic (ranunculaceous); those of adult leaves are various (Moncontié). Stomata are usually diacytic (caryophyllaceous) in a number of species, including *P. lanceolata* and *P. Psyllium,* but they are rarely so in *P. major.* They may be distributed either on both surfaces of the leaf (e.g., as in *P. lanceolata, P. major,* and *P. Psyllium*) or (as in two extraregional species) only abaxially (Metcalfe & Chalk). In *P. lanceolata* and the extraregional *P. altissima* L. stomatal size appears to be positively correlated with chromosome number (Moncontié).

The floral anatomy of *Plantago lanceolata, P. major,* and *P. Rugelii* has been studied by Henderson, whose observations suggested that the bract in *Plantago* actually represents a fifth sepal. Henderson observed, among numerous other things, that the stamens separate from the receptacle as a ring of tissue (remaining connate for some distance up the ovary) and are never fused to the corolla in *P. lanceolata* and *P. major*; my own observations, however, reveal that they are indeed epipetalous, as she correctly indicated for *P. Rugelii.*

The ovule in *Plantago* has a single, massive integument and is tenuinucellar (the archesporial cell develops directly into the megaspore mother cell). It has been described as anatropous by Cooper (for *P. lanceolata,* although his illustration showed it to be more similar to what is usually considered hemianatropous), anacampylotropous by Misra (1964, for *Plantago*), hemianatropous to anatropous by Davis (for the family), anatropous to hemitropous by Cronquist (1981, for the family), and more or less anatropous, erect, or anacampylotropous by Corner (for the family). Ovule and seed development in *P. lanceolata* have been described in great detail by Cooper (see also Davis; Misra, 1964), who stated that the megagametophyte in this species is of the Polygonum type. Although Cooper also indicated that the basal cell of the zygote forms the suspensor, Davis stated that the embryogeny is of the Onagrad type. The presence of both micropylar and chalazal haustoria in the developing seed was noted above (family discussion).

Circumscissile dehiscence of the fruit occurs in such disparate genera as *Plantago* and *Celosia* (Amaranthaceae), *Anagallis* and *Centunculus* (= *Anagallis*) (Primulaceae), *Portulaca* and *Lewisia* (Portulacaceae), and *Hyoscyamus* (Solanaceae). In each of the species of *Plantago* studied by Rethke (including *P. major* and *P. pusilla*), the cells near the region of future dehiscence remain meristematic through much of fruit maturation. These cells are smaller and have thinner walls than adjacent epidermal and/or subepidermal cells. Dehis-

cence results from the breaking and separation of cells in this zone of mechanical weakness and occurs as the drying capsule shrinks against the mature, unyielding seeds (see also Lamba & Gupta).

The extent to which genotype (vs. environmental factors) determines phenotype, including morphological oddities, has received considerable attention. Evidence has suggested that while branched spikes are under genetic control in *P. lanceolata* (Weatherwax; cf., however, Yamaura) and *P. major* (Hammarlund), they seem to result from external factors in *P. Rugelii* (Weatherwax). The lengths of scapes, capsules, seeds, and bracts (as well as the number of flowers produced) were all found to be positively correlated with plant size in *P. aristata* (Goodwin), which is evidently not genetically determined. It is notable that depauperate plants sometimes produce lowermost bracts that do not exceed the flowers they subtend, and that they may thus rather closely resemble several other species of sect. GNAPHALOIDES. In a series of long-range experiments involving both cuttings and seedlings, Marsden-Jones and Turrill found that plant size and peduncle pubescence in *Plantago major* were mostly determined by the soil in which the plants were grown (cf., however, Warwick & Briggs, 1979).

A number of studies have been undertaken to determine the relationship between phenotype and ploidy level in *Plantago*. Chandler (1954) showed that pollen size, seed size, quantity of mucilage, and plant vigor are all greater in colchicine-induced tetraploids (compared to the corresponding diploids) in *P. rhodosperma, P. Wrightiana,* and the extraregional *P. ovata*. In *P. ovata* such treatment resulted in larger leaves with generally larger cells, larger stomata, and broader epidermal hairs (Chandler & Barton). Several physiological differences were also noted, including the fact that tetraploids are, in general, developmentally slower than diploids. It is also interesting that the amount of aucubin (see family discussion) did not differ between the two groups. In other studies involving extraregional species, Rahn (1954) discovered that in *P. media* the seed number per capsule, scape length, and leaf size are all greater in natural tetraploids than in diploids (although pollen diameter and stomatal size do not differ), and Böcher *et al.* found in *P. Coronopus* L. that the anthers, flowers, and plants themselves are larger in natural hexaploids than in diploids.

Hybrids involving species of *Plantago* represented in the Southeast have apparently not been encountered (with the exception of the artificially produced *P. cordata* × *P. eriopoda* [Tessene, 1969]). Artificial crosses between *P. major* (sect. PLANTAGO) and *P. lanceolata* (sect. LANCIFOLIA) were unsuccessful (Rahn, 1957). In fact, hybrids involving these two species, either together or with other species, are not known (Sagar & Harper, 1964). No hybrid in which *P. major* was a parent has been reported, and the identity of herbarium specimens of a putative hybrid between *P. lanceolata* and the extraregional *P. media* (sect. LAMPROSANTHA Dcne. of subg. PLANTAGO) is doubtful. All attempts to produce artificial hybrids between *P. media* and either *P. major* or *P. lanceolata* have failed. Attempted crosses between extraregional species in sect. LAMPROSANTHA and those in sects. PLANTAGO, LANCIFOLIA, and CORONOPUS have also been unsuccessful (Rahn, 1957). Also among species not occurring in the Southeast, natural introgressive hybridization was reported in subg. CORONOPUS sect.

MARITIMA H. Dietr. (Cartier, 1971, 1972), and a high degree of interfertility was observed in subg. PSYLLIUM sect. MONTANA Barn. when artificial crosses involved plants with the same chromosome number (Cartier, 1973).

The occurrence of perfect and carpellate flowers on separate plants (gynodioecy) has been observed, investigated, and discussed since the time of Darwin. *Plantago lanceolata,* in particular, has been the subject of a number of investigations (see Bartlett, Ludwig, and Ross [1969]). Ross proposed that there are dominant alleles at two loci for perfect flowers, so double homozygous recessive individuals produce only carpellate flowers (cf., however, Atal, Van Damme & Van Delden, and Krohne *et al.* regarding a possible cytoplasmic effect). Because such individuals contribute genes to subsequent generations through ovules only, it is reasonable to postulate the existence of a compensatory mechanism by which carpellate-flowered plants are maintained in populations in which plants with perfect flowers contribute genes through both ovules and pollen and are therefore presumably at a selective advantage. Krohne *et al.* determined, in fact, that in natural populations (in northern California) carpellate plants generally produce more seeds than do those with perfect flowers (see also Primack, 1978).

Plantago lanceolata is also self-incompatible, even though such a system might appear to reinforce the process of outcrossing unnecessarily. Investigations by Ross (1973) suggested that at least four alleles at a single locus are involved, and that incompatibility results if the pollen has either of the alleles present in the style. (Unlike most other angiosperms with trinucleate pollen, the incompatibility is gametophytic.) Ross (1973) argued that matings between wholly perfect or wholly carpellate progeny (which could result from individual maternal parent plants with perfect or carpellate flowers, respectively) would be limited by self-incompatibility in the first case (there would be no limitation on such crosses under gynodioecy alone) and prevented by gynodioecy in the second (a portion of such crosses would be possible under the incompatibility system alone). In this way the two systems would be mutually reinforcing.

Plantago is usually considered to be primarily wind pollinated, at least in those species with chasmogamous flowers, and a majority of the evidence seems to bear this out. Many of the traits usually associated with anemophily (flowers proterogynous, small, unattractive, scentless; stigmas large, pubescent; anthers large, versatile on long filaments; and pollen spheroidal, dry, relatively smooth, with little variation in size) are found in species of *Plantago.* For example, on the basis of data gathered by Bassett and Crompton from North American plants, Primack (1978) demonstrated that variation in mean pollen diameter was greater among species with cleistogamous flowers than among those with chasmogamous ones. This presumably reflects selection against pollen that is either too large or too small (see also Proctor & Yeo).

Some species of *Plantago* appear to be at least partly entomophilous (but, as Proctor & Yeo have pointed out, bees sometimes collect pollen from plants that are anemophilous). Clifford stated that in Britain *P. lanceolata* is considered to be wind pollinated, but plants of it are regularly worked by honey bees for pollen whenever conditions are warm enough and a sufficient number of spikes are flowering within a few feet of one another. A more elaborate study

of insect pollination in this species in the Netherlands (Stelleman & Meeuse) attempted to prove that pollen is actually transferred to the stigmas by flies of the genera *Melanostoma* and *Platycheirus* (Diptera: Syrphidae). Spikes of a group of donor plants were dusted with stained pollen of *P. lanceolata*. This pollen was later detected on both the flies and the stigmas of receptor plants located in a separate group upwind, while only negligible amounts of it were found on the donor plants' side of test slides placed between the two groups of plants.

Several investigations of reproductive biology have involved species of *Plantago* in the Southeast. Primack (1979) estimated that "reproductive output" is greater among annuals (vs. perennials), spring (vs. summer) annuals, and weedy (vs. nonweedy) perennials. Primack and Antonovics (1982) later found that in "reproductive effort" eight populations of *P. lanceolata* from the central Piedmont of North Carolina had a range of values comparable to that obtained by Primack (1979) for various perennial and/or weedy species of *Plantago*, but less than that determined for annual species (although the degree of genetic control was not clearly established). Primack (1980) also determined that phenotypic variation in *Plantago*, as measured by several criteria (number of inflorescences, number of capsules per inflorescence, number of seeds per capsule, and weight per seed), is no less in rare species than in more widespread ones. Significant differences in all of these measures except seed number per capsule were later observed under controlled conditions in *P. lanceolata* (Primack & Antonovics, 1981).

Studies involving *Plantago lanceolata* have shown that these plants may become physiologically adapted to very local conditions. Among populations in the Southeast, Wu and Antonovics (1976) demonstrated a greater tolerance to lead by roadside (vs. nonroadside) individuals, and Pollard showed essentially the same kind of response to zinc, copper, arsenic, and lead at sites contaminated with these metals. In contrast to various authors who have suggested that the wide geographic ranges characteristic of many weedy species are primarily the result of broad temperature optima for photosynthesis, Teramura and Strain demonstrated that substantial differences exist in the photosynthetic response to temperature among populations growing in relatively close proximity (eight meters to ten kilometers apart). Plants cloned from leaves taken from a shaded population were more sensitive to temperature extremes than were those propagated from open and sun-flecked populations that were exposed to much greater diurnal and seasonal fluctuations in temperature. Plants from the open population had much greater light-saturated rates of photosynthesis as well.

Plantago pollen has been helpful in studies regarding the effects of human activity on vegetation. Godwin (1975) pointed out that the increase in the number of records of *P. major* and *P. lanceolata* in British postglacial sediments corresponds to the progress of deforestation and the spread of agriculture by Neolithic man. (There are no corresponding increases involving such less weedy species as *P. media* and *P. maritima* L.) In the Vosges region of France, the degree of aforestation and cultivation is reflected in the relative abundance of the pollen of *P. lanceolata* in surface samples (Janssen).

The rather substantial, but frequently underestimated, economic significance of *Plantago* has been thoroughly discussed by Hammond. Several species, but especially *P. lanceolata* and *P. major,* are well known and noxious lawn weeds that also compete with crop plants for light, space, and nutrients (see Hammond; Higbee & Lee). Inadvertent dissemination of these plants results from *Plantago* seeds being unavoidably harvested with (and difficult to separate from) crop seeds. The leaves of *Plantago* do not dry readily and can therefore contribute to spoilage in hay that is sufficiently contaminated (Gill & Vear). *Plantago* species also act as hosts to a variety of viruses and (other) organisms known to cause disease in crops including beets, potatoes, turnips, cucumbers, tomatoes, broad beans, and tobacco. Precisely how this translates into economic loss is largely a matter of speculation at present.

Plantago lanceolata is sometimes fed to livestock as a mineral supplement, and it is still grown in the Netherlands for use in herbal remedies. *Plantago major* has also been used in this way for a variety of medicinal problems. The mucilaginous seeds of *P. Psyllium* and related species ("psyllium" seeds) act as a mild laxative and are harvested from crops raised specifically for this purpose. Chandler (1954) reported that almost four million pounds of psyllium seeds were imported into this country in 1953 and discussed the possibilities of domestic production for use of the mucilage in pharmaceutical preparations and as basic stabilizers in making ice cream, in printing and finishing, and in setting lotions (see also Morton). According to the United States Department of Agriculture, Foreign Agricultural Service, over 12 million pounds of psyllium seeds were imported into this country in 1981, at a value of over nine million 1981 dollars.

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dynamics, and response to human manipulations (including herbicides and other chemicals) and parasites.]

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D'ARCY, W. G. Plantaginaceae. *In*: R. E. WOODSON, JR., & R. N. SCHERY, eds., Fl. Panama. Ann. Missouri Bot. Gard. **58**: 363–369. 1971. [Three spp.; *P. lanceolata* not reported from below 3300 ft, *P. major* from as low as 200 ft; neither considered common enough to be a nuisance.]

DIETRICH, H. Studien an cubanischen Plantaginaceae. Wiss. Zeitschr. Friedrich Schiller Univ. Jena Math. Nat. **28**: 701–708. 1979. [*P. lanceolata, P. major, P. Rugelii* at or near sea level; floral morphology, cytology, palynology; illustration, map of distribution in Cuba.]

DODDS, J. G. *Plantago Coronopus* L. Jour. Ecol. **41**: 467–478. 1953. (Systematics and biology; cementing of seed to substrate by mucilage thought to be advantageous in germination.]

DOWLING, R. E. The structure of the ovary in the genus *Plantago* L. — I. The British species. Jour. Linn. Soc. Bot. **50**: 323–336. 1936. [*P. lanceolata, P. major*; variation in seed number in *P. major* suggests the ovary is of little value in defining either sections or species.]

EAMES, A. J. Morphology of the angiosperms. *Frontisp.* + xiii + 518 pp. New York, Toronto, and London. 1961. [Anemophily in *Plantago*; genus provides example of reduction to one flower from racemose clusters; leaves phyllodes.]

ESAU, K. Plant anatomy. xii + 735 pp. New York and London. 1953. [*Plantago*, 421

(striate venation), 455 (leaf development), 581 (circumscissile dehiscence), 604 (mucilaginous seeds).]

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FUJIWARA, I. Karyotype analysis in *Plantago* I. (In Japanese; English summary.) Kromosomo **27/28:** 962–968. 1956. [*P. major.*]

———. Karyotype analysis in *Plantago* II. (In Japanese; English summary.) Jap. Jour. Genet. **31:** 184–191. 1956. [*P. lanceolata, P. Psyllium, P. virginica*; karyotypes of subg. *Psyllium* essentially similar to those of subg. *Plantago*; *P. virginica* an allotetraploid; *P. Psyllium* and *P. indica* "partially related" karyotypically.]

GILL, N. T., & K. C. VEAR. Agricultural botany. viii + 636 pp. London. 1958. [Plantaginaceae, 451; seedlings of *P. major* and *P. lanceolata* illustrated, 496, 497.]

GODFREY, R. K. *Plantago cordata* still grows in Georgia. Castanea **26:** 119, 120. 1961. [Confirmed for Gordon Co.]

——— & J. W. WOOTEN. Aquatic and wetland plants of southeastern United States. Dicotyledons. x + 933 pp. Athens, Georgia. 1981. [*Plantago,* six spp., 710–712.]

GODWIN, H. Age and origin of the 'Breckland' heaths of East Anglia. Nature **154:** 6, 7. 1944. [Pollen of *P. lanceolata* indicates origin in Neolithic forest clearance.]

GOODWIN, R. H. Variation in a natural population of *Plantago aristata.* Bull. Torrey Bot. Club **76:** 109–115. 1949.

GORENFLOT, R. Introgression, polymorphisme et taxonomie chez les Plantaginacées. Adansonia, II. **4:** 393–417. 1964. [Natural and artificial hybridization between and within *P. Coronopus* and *P. macrorhiza* Poiret.]

GREGOR, J. W. Experimental taxonomy IV. Population differentiation in North American and European sea plantains allied to *Plantago maritima* L. New Phytol. **38:** 293–322. 1939. [Spike density, sepal length/width, growth habit, scape length follow an ecological gradient; leaf pubescence varies geographically from western North America to central Europe.]

GRIFFITHS, B. M. Growth experiments on *Spergula* and *Plantago.* Jour. Bot. London **60:** 228–230. 1922. [*P. lanceolata* var. *sphaerostachya* Roehl. an environmental modification; a form of *P. major* with large inflorescences (and other characters) suspected of being under control of a recessive allele.]

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HAMMARLUND, C. Über die Vererbung anormaler Ähren bei *Plantago major.* (English summary.) Hereditas **2:** 113–142. 1921. [Alleles for branched spikes with leaves instead of bracts considered recessive.]

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HARPER, R. M. Notes on *Plantago,* with special reference to *P. cordata.* Castanea **9:**

121–130. 1944. [*P. elongata, P. heterophylla,* and *P. pusilla*; historical notes on the occurrence of *P. cordata* in the Southeast.]

HAWTHORN, W. R., & P. B. CAVERS. Population dynamics of the perennial herbs *Plantago major* L. and *P. Rugelii* Decne. Jour. Ecol. **64:** 511–527. 1976.

——— & ———. Dry weight and resource allocation patterns among individuals in populations of *Plantago major* and *P. Rugelii.* Canad. Jour. Bot. **60:** 2424–2439. 1982. [Greater overwintering survival and longevity observed in natural populations of *P. Rugelii.*]

HENDERSON, L. B. Floral anatomy of several species of *Plantago.* Am. Jour. Bot. **13:** 397–405. 1926.

HIGBEE, E. C., & A. LEE. Drug and medicinal crops. Pp. 127–160 *in* C. M. WILSON, ed., New crops for the New World. New York. 1945. [Psyllium, 148, 149; requires heavy fertilization when grown commercially.]

HILLEBRAND, W. Flora of the Hawaiian Islands: a description of their phanerogams and vascular cryptogams. *Frontisp.* + xcvi + 673 pp. + *4 maps* (incl. 3 foldouts). London, New York, and Heidelberg. 1818. [*P. major* introduced and said to have 6–8 inch petioles and 1.5–2 foot spikes on the high pasture lands; two native species endemic; cf. ROCK.]

HITCHCOCK, C. L., & A. CRONQUIST. Flora of the Pacific Northwest. xix + 730 pp. Seattle and London. 1973. [Plantaginaceae, 447, 448.]

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———. Mucilage-producing cells in the seed coat of *Plantago ovata*: developmental fine structure. *Ibid.* **57:** 1197–1206. 1970. [Anatomical, ultrastructural, and histochemical changes during development; transmission electron micrographs.]

HYDE, H. A., & D. A. WILLIAMS. Studies in atmospheric pollen III. Pollen production and pollen incidence in ribwort plantain (*Plantago lanceolata* L.). New Phytol. **45:** 271–277. 1946. [Low temperatures delay or suppress daily flowering time; estimated that almost 94 percent of all pollen liberated becomes airborne.]

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KUNKEL, G. Über einige morphologische Anomalien bei *Plantago lanceolata* L. und anderen Pflanzen in Valdivia (Südchile). Beitr. Biol. Pflanzen **34:** 509–530. 1958. [Branched inflorescences and rosette formation on scapes.]

KUO, S. H., & W. H. MURDY. The response of city and rural populations to an urban environment. (Abstr.) ASB Bull. **20:** 65. 1973. [Garden experiments with *P. aristata.*]

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LAMBA, L. C., & V. GUPTA. Anatomy of circumscissile dehiscence in *Plantago ovata* Forsk. Curr. Sci. Bangalore **50:** 541–543. 1981. [Scanning electron micrographs of capsule.]

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LEBEDEV-KOSOV, V. I. Flavonoids of *Plantago major*. Chem. Nat. Compds. **12:** 730. 1977. [Translation of Khimiya Prirodnykh Soedinenii **6:** 812, 813. 1976; evidently the first report of flavonoids in the Plantaginaceae (apigenin and two luteolins).]

LONG, R. W., & O. LAKELA. A flora of tropical Florida. xvii + 962 pp. Coral Gables, Florida. 1971. [*P. aristata, P. lanceolata, P. major,* and *P. virginica.*]

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———. North American Plantaginaceae—III. *Ibid.* **36:** 515–530. 1909. [*P. pusilla* compared with *P. elongata, P. heterophylla,* and *P. hybrida*; cf. GODFREY & WOOTEN.]

MORTON, J. F. Major medicinal plants[.] Botany, culture, and uses. xix + 431 pp. Springfield, Illinois. 1977. [*Plantago,* 323–332.]

MULLIGAN, G. A., & J. N. FINDLAY. Reproductive systems and colonization in Canadian weeds. Canad. Jour. Bot. **48:** 859, 860. 1970. [Bagged flowers of *P. major* set viable seeds (i.e., the plants are self-compatible and/or apomictic).]

MUNZ, P. A. A California flora. vii + 1681 pp. Berkeley, Los Angeles, and London. 1959. [16 spp. of *Plantago,* 405–409; also 78, 79 in Supplement (224 pp.), 1968.]

NEVA, A. C., & E. B. FISCHER. A comparative pharmacognostical study of *Plantago Purshii* R. & S. and *Plantago aristata* Michx. seeds with the present N. F. VIII *Plantago* seeds. Jour. Am. Pharm. Assoc. Sci. Ed. **38:** 34–41. 1949. [Detailed descriptions of seed structure.]

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ONO, R. Studies of the chromosomes of *Plantago* III. Chromosomes of *Plantago lanceolata* L. Jap. Jour. Genet. **29:** 138, 139. 1954. [Meiotic divisions in pollen mother cells were regular (six bivalents); cf., however, MCCULLAGH regarding chromosome morphology.]

PANIGRAHI, G. A note on *Plantago exigua* (Plantaginaceae) and certain related taxa. Kew Bull. **30:** 669–673. 1975 [1976].

POE, I. A revision of the *Plantago patagonica* group of the United States and Canada. Bull. Torrey Bot. Club **55:** 406–420. 1928. [". . . plants growing in full sun tend to

have shorter, more vigorous stems and wider leaves, yet bracts [length and shape] remain fairly constant." Jacquin's description and plate of *P. patagonica* did not conform to any species then known in North America, yet specimens of *P. patagonica* from Argentina were similar to *P. Purshii.* Type of *P. Wrightiana* considered to belong to *P. Hookeriana* var. *nuda.*]

POLLARD, A. J. Diversity of metal tolerances in *Plantago lanceolata* L. from the southeastern United States. New Phytol. **86:** 109–117. 1980.

PRIMACK, R. B. Evolutionary aspects of wind pollination in the genus *Plantago* (Plantaginaceae). New Phytol. **81:** 449–458. 1978. [Carpellate plants produced more inflorescences and heavier seeds than did perfect ones; differences in seed weight attributed to the high cost of pollen production.]

———. Regulation of seed yield in *Plantago.* Jour. Ecol. **66:** 835–847. 1978. [Includes data from all of the southeastern species.]

———. Reproductive effort in annual and perennial species of *Plantago* (Plantaginaceae). Am. Nat. **114:** 51–62. 1979. [Includes data from natural populations and herbarium specimens representing all of the southeastern species.]

———. Phenotypic variation of rare and widespread species of *Plantago.* Rhodora **82:** 87–95. 1980. [Includes data from all of the southeastern species.]

——— & J. ANTONOVICS. Experimental ecological genetics in *Plantago.* V. Components of seed yield in the ribwort plantain *Plantago lanceolata* L. Evolution **35:** 1069–1079. 1981. [In plants under controlled conditions, significant differences in inflorescence number per plant, capsule number per inflorescence, and seed weight, but not in seed number per capsule.]

——— & ———. Experimental ecological genetics in *Plantago.* VII. Reproductive effort in populations of *P. lanceolata* L. *Ibid.* **36:** 742–752. 1982.

PROCTOR, M., & P. YEO. The pollination of flowers. 418 pp. + *56 black & white + 4 color pls.* New York. 1972.

RADFORD, A. E., H. E. AHLES, & C. R. BELL. Manual of the vascular flora of the Carolinas. 1xi + 1183 pp. Chapel Hill, North Carolina. 1968.

RAHN, K. Experimental and cytological studies in *Plantago media.* Bot. Tidsskr. **51:** 300–307. 1954.

———. Chromosome numbers in *Plantago. Ibid.* **53:** 369–378. 1957. [Seeds referred to the hybrid *P. media* × *lanceolata* always yielded one or the other of the parent species; unsuccessful crosses attempted between *P. lanceolata, P. major,* and *P. media* (and other species); evidence for apomixis; two of 42 "strains" of *P. lanceolata,* $2n = 12$, reported as aneuploids, $2n = 13$.]

———. *Plantago* section *Virginica.* Dansk Bot. Ark. **30**(2): 1–180. 1974. [28 spp.]

———. Plantaginaceae. Fl. Ecuador **4:** 23–38. 1975. [Ten spp. of *Plantago,* including *P. lanceolata* and *P. major,* none at low elevations.]

———. Nomenclatorial changes within the genus *Plantago* L., infraspecific taxa and subdivisions of the genus. Bot. Tidsskr. **73:** 106–111. 1978a. [Subg. *Plantago,* 11 sections, need of revision noted; subg. *Coronopus* established, two sections; subg. *Psyllium,* seven sections.]

———. *Plantago* ser. *Gnaphaloides* Rhan[,] a taxonomic revision. *Ibid.* **73:** 137–154. 1978b.

READ, D. J., H. K. KOUCHEKI, & J. HODGSON. Vesicular-arbuscular mycorrhiza in natural vegetation systems I. The occurrence of infection. New Phytol. **77:** 641–653. 1976. [Seedlings of *P. lanceolata* with mycorrhizal fungi.]

RETHKE, R. V. The anatomy of circumscissile dehiscence. Am. Jour. Bot. **33:** 677–683. 1946. [*P. major, P. pusilla.*]

REZK, M. R. Seed structure as a phylogenetic criterion. A case of *Plantago* seed. Egypt. Jour. Bot. **23:** 51–62. 1980. [*P. lanceolata, P. major, P. virginica.*]

ROCK, J. F. The genus *Plantago* in Hawaii. Am. Jour. Bot. **7:** 195–211. 1920. [*P. lanceolata, P. major,* and *P. virginica* introduced; two native species endemic.]

RODMAN, J. E. Divergence, convergence, and parallelism in phytochemical characters:

the glucosinolate-myrosinase system. Pp. 43–79 *in* D. A. YOUNG & D. S. SEIGLER, eds., Phytochemistry and angiosperm phylogeny. New York. 1981. [Myrosin cells (protein-rich idioblasts in which myrosinase is thought to be concentrated) reportedly absent from the Plantaginaceae, even though hydrolysis products of glucosinolates have been reported from leaves of certain *Plantago* species (including *P. major*).]

ROSS, M. D. Digenic inheritance of male sterility in *Plantago lanceolata*. Canad. Jour. Genet. Cytol. **11:** 739–744. 1969. [Nearly continuous variation between plants with only perfect flowers and those with only carpellate ones.]

———. Breeding systems in *Plantago*. Heredity **25:** 129–133. 1970. [12 spp., including *P. aristata* and *P. rhodosperma* (assumed to be self-compatible because of cleistogamy), *P. lanceolata* (both gynodioecious and self-incompatible), *P. major* (both gynodioecious and self-compatible, at least locally), and *P. Wrightiana* (assumed to be self-compatible because fertilization prior to corolla expansion).]

———. Inheritance of self-incompatibility in *Plantago lanceolata*. *Ibid.* **30:** 169–176. 1973.

RYMKIEWICZ, A. Studies on the species of the genus *Plantago* L. with reference to carpology and chemotaxonomy. (In Polish; English summary.) Monogr. Bot. **57:** 71–103. 1979. [Plants of *P. lanceolata, P. major, P. Psyllium,* and other spp. cultivated for four years; illustrations of seeds and of transverse sections of endosperm and testa; aucubin content of seeds.]

SAGAR, G. R., & J. L. HARPER. Factors affecting the germination and early establishment of plantains (*Plantago lanceolata, P. media* and *P. major*). Pp. 236–245 *in* J. L. HARPER, ed., The biology of weeds. Oxford. 1960.

——— & ———. Controlled interference with natural populations of *Plantago lanceolata, P. major* and *P. media*. Weed Res. **1:** 163–176. 1961. [Grasses affect size and constitution of *Plantago* populations, at least partially by acting on seedlings.]

——— & ———. Biological flora of the British Isles[;] *Plantago major* L., *P. media* L. and *P. lanceolata* L. Jour. Ecol. **52:** 189–221. 1964. [Extensive and detailed biological information; rosette clumping in *P. lanceolata* due to axillary shoot formation on underground rhizomes.]

SHADOWSKY, A. E. Embryological researches on *Plantago major* L. f. *phyllostachya* Wallr. (Russian summary.) Bull. Soc. Nat. Moscou II. **32:** 234–259. 1924. [Pollen, ovules, seeds.]

SHEAR, G. M. *Plantago arenaria*. Claytonia **2:** 14. 1935. [One individual of *P. arenaria* found near Blacksburg, Virginia.]

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ANATOMY OF STEM ABSCISSION IN THE GENUS SMILACINA (LILIACEAE)

James V. LaFrankie, Jr.

Abscission, the shedding of organs or parts, is a phenomenon found in many taxa of both higher and lower plants. The abscission zone associated with the leaves, fruits, and stems of dicotyledons of the Temperate Zone has received much attention, and comparative anatomical studies have been particularly extensive (Lee, 1911; Pfeiffer, 1928; Kozlowski, 1973; Addicott, 1982). An abscission zone typically includes two distinct anatomical regions: a discrete separation layer responsible for the actual detachment of the abscised organ; and a protective layer that seals the parent axis, preventing water loss and the entry of pathogens.

While these two anatomical layers have been found in many dicotyledons, the occurrence of similar layers in monocotyledons is less well known. Separation layers have been found at the leaf insertion of some palms (La Floresta, 1904; Tomlinson, 1962) and in the fronds of the Lemnaceae (Witztum, 1974; Newton *et al.,* 1978). Protective tissues not necessarily associated with the separation of parts occur in many species of monocotyledons. Philipp (1923) classified the protective layers into three types: a metacutis, a simple periderm, and a storied periderm. Philipp, however, was not concerned with the condition or situation in which a plant developed protective layers, and it is unclear when—if ever—these layers are related to abscission.

Stem abscission occurs in many monocotyledons of the Temperate Zone that grow sympodially. Such plants form a stem-abscission zone either at or below ground level as part of their normal seasonal cycle of shoot senescence and shoot regeneration. In this article, the developmental anatomy of abscission is described in *Smilacina racemosa* (L.) Desf. (Liliaceae), a good example of a sympodially regenerating herb with a perennial rhizome. For comparative purposes the abscission scars of four other species in the genus (*Smilacina japonica* A. Gray, *S. stellata* (L.) Desf., *S. scilloidea* Martens & Galeotti, and *S. paniculata* Martens & Galeotti) are examined, although in less detail.

The annual shoot of *Smilacina racemosa* is determinate and consists of a horizontal rhizome and an upright leafy axis. The aerial parts live only a single growing season; they are subsequently replaced by a renewal shoot that develops from a lateral bud found at the base of the leafy axis. The renewal shoot grows horizontally for 2–3 cm before turning upward and forming an overwintering bud that contains the preformed leafy shoot for the following year. This sequence of determinate growth and lateral regeneration is repeated annually.

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Although the aerial portion of each shoot is lost in autumn, the underground part lives for ten or more years; the perennial rhizome is thus a sympodium composed of the persistent basal portions of old shoots. A prominent scar marks the location of each of the abscised parent axes and therefore also the annual growth increment (FIGURE 1).

MATERIALS AND METHODS

The abscission zone in *Smilacina racemosa* was studied in two ways: as it developed without disturbance in local populations at Harvard Forest, Petersham, Massachusetts; and as it developed in response to clipping of the aerial shoot. Previous experience showed that the abscission zone appears naturally during the late summer or fall prior to senescence of the aerial shoot, but developmental studies are difficult because the phenology of individual plants is quite variable. Abscission can be induced in midsummer by cutting the aerial stem just below the lowest leaf, approximately 25 cm above the ground. Such experimentally manipulated plants are advantageous because the abscission zone develops uniformly in them after the aerial stem has been cut.

The aerial shoots of 25 plants within a natural population were cut in this manner on 27 July 1983, and the rhizomes of these plants were subsequently excavated, five at a time, at 0, 3, 7, 14, and 28 days after cutting. Untreated control plants were also collected on each occasion. Additional collections were made throughout the spring, summer, and fall of 1982 and 1983 to extend knowledge of the natural phenology of the protective process.

Fresh material was examined microscopically in transverse and longitudinal hand sections. Additional material was fixed in FAA, dehydrated in TBA, embedded in paraffin, and sectioned at 8 μm. Sections were either stained in safranin and alcian green or subjected to several microchemical tests. The presence of suberin was verified by Sudan IV and the IKI–sulfuric acid test (Johansen, 1940). Lignin was detected by both the HCl–potassium permanganate test (Maule's reagent) according to Johansen (1940) and the HCl-phloroglucinol reaction. In the latter method sections were first dehydrated in eth-

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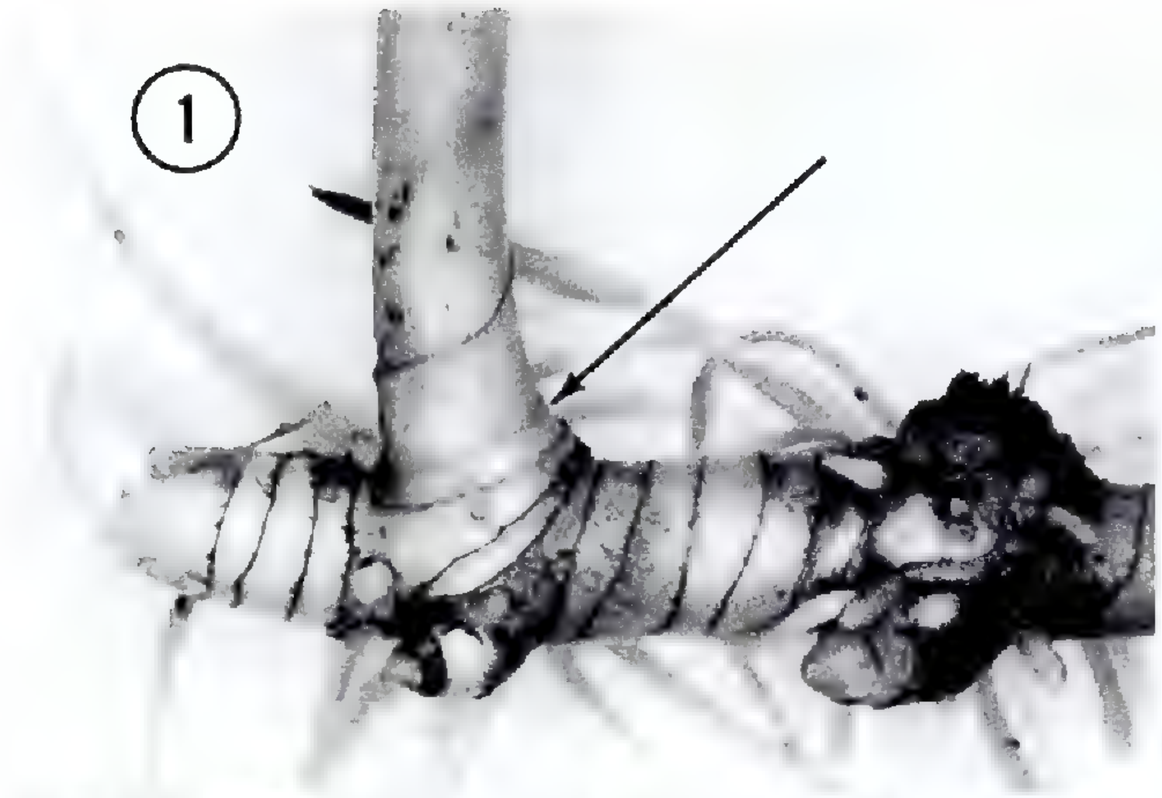
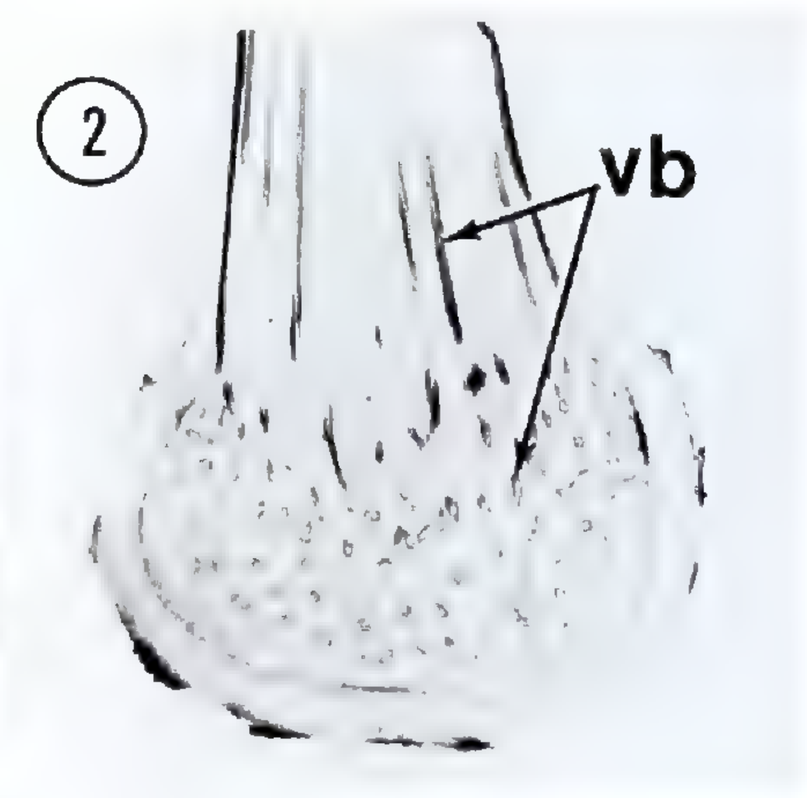
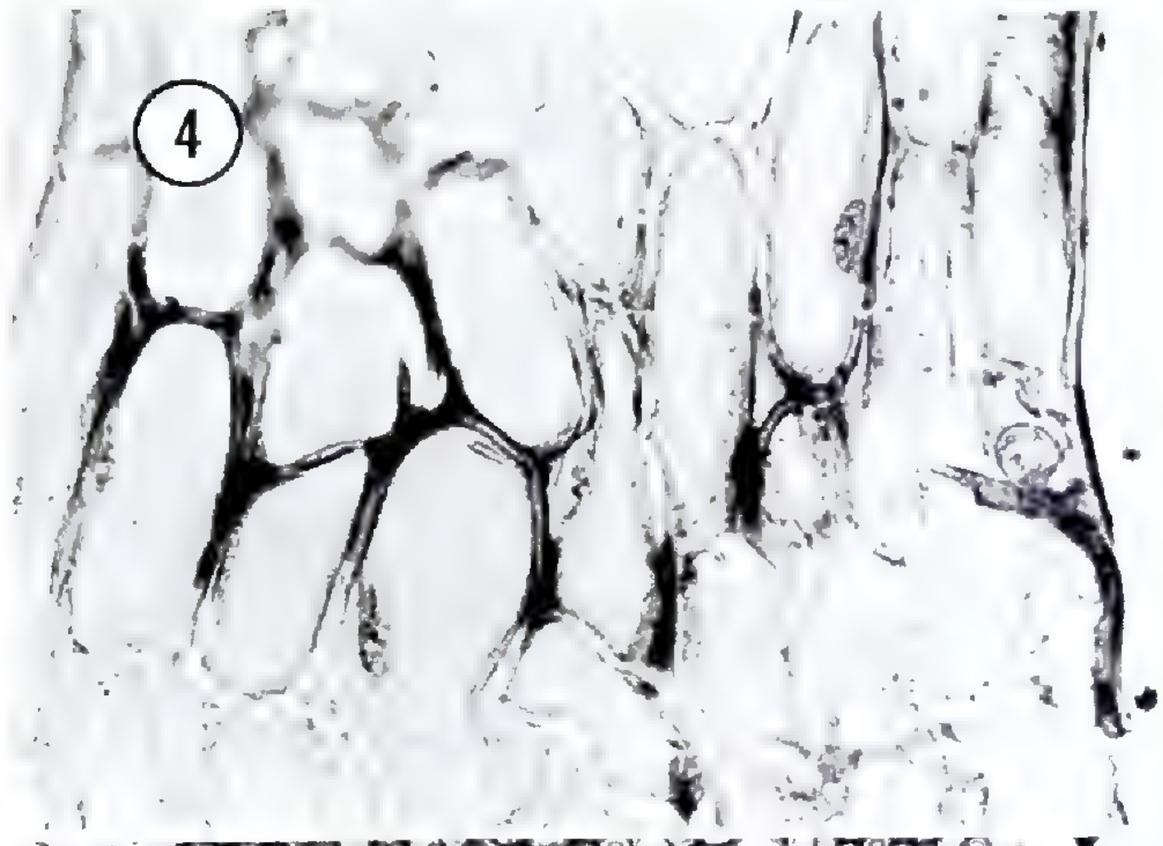
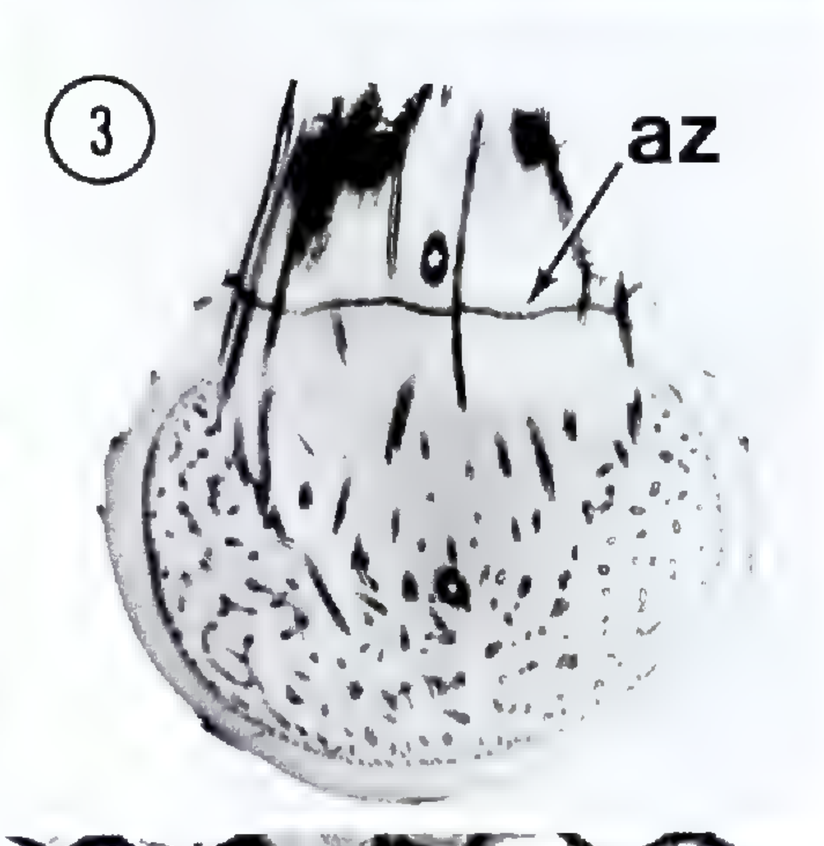
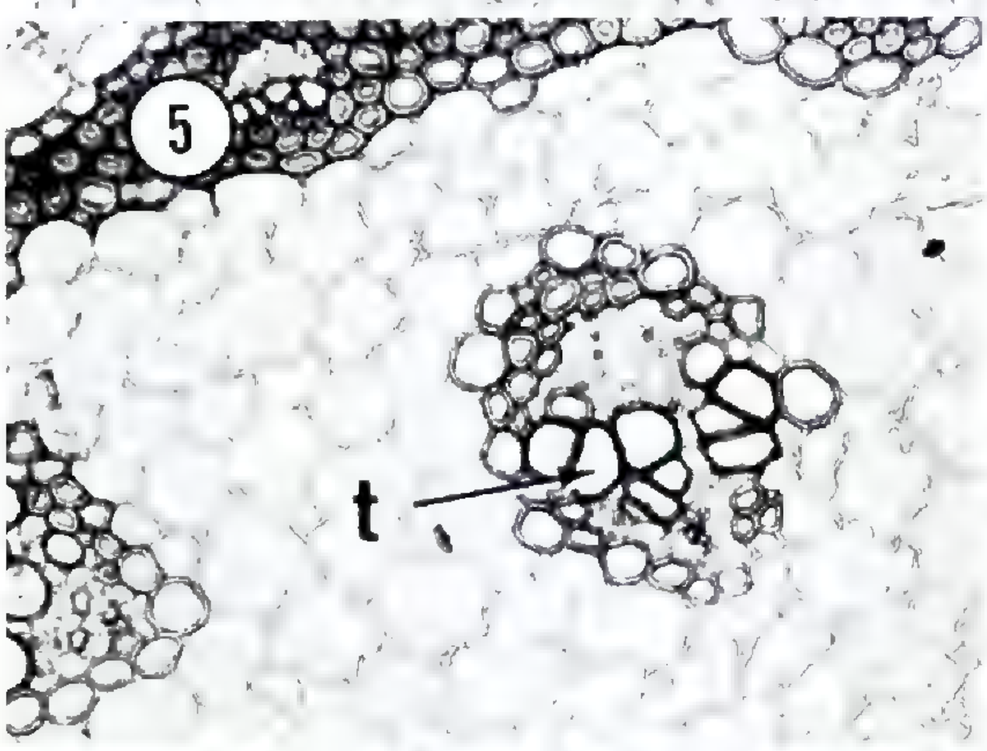
FIGURES 1–8. *Smilacina racemosa,* development of abscission zone. 1–3, 8, untreated control plants; 4–7, abscission induced; all sections stained using HCl-phloroglucinol method. 1, rhizome (August 30), × 0.9; abscission zone visible at base of aerial shoot (arrow), renewal shoot to left, scar of previous year's aerial shoot to right. 2, thick longitudinal section through stem base (June 30), × 1.8, showing vascular bundles (vb). 3, thick longitudinal section through stem base (August 30), × 1.8, showing abscission zone (az). 4, longitudinal section through stem base (7 days after cutting), × 125, showing first stage of abscission; some cell walls lignified. 5, transverse section through stem base at level of abscission zone (7 days after cutting), × 75, showing normal vascular bundle before occlusion of tracheids (t). 6, transverse section through stem base at level of abscission zone (14 days after experimental cutting), × 75, parenchyma cell walls heavily lignified and tracheids (t) occluded. 7, longitudinal section through stem base (14 days

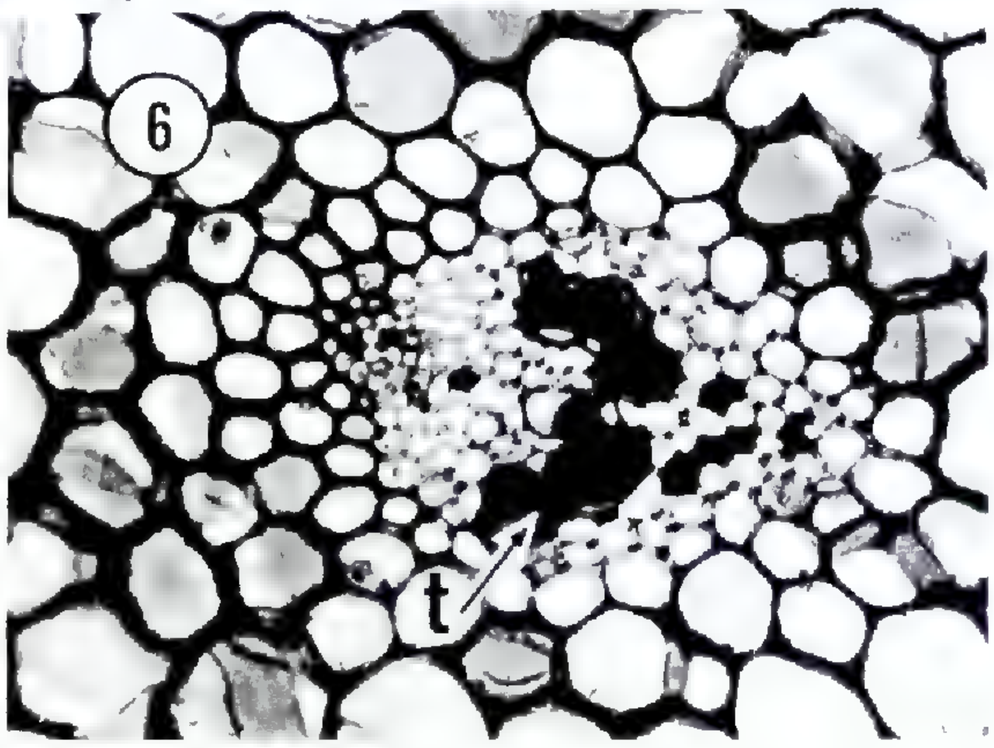


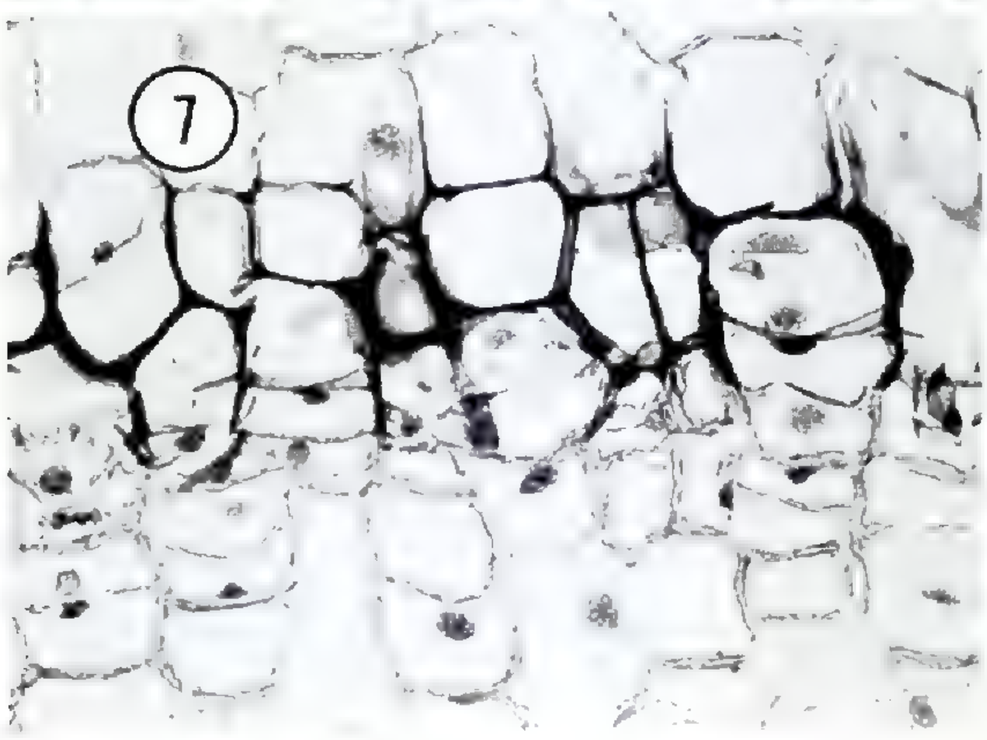












after experimental cutting), × 80, showing newly divided cells proximal to ligno-suberized layer. 8, longitudinal section through stem base (2 years after loss of aerial stem), × 80.

TABLE 1. **Voucher specimens.**

SPECIES	VOUCHER
Smilacina racemosa	U.S.A., Massachusetts, Petersham, *LaFrankie 138.*
S. stellata	U.S.A., Massachusetts, Plum Is., *LaFrankie 76.*
S. japonica	Japan, Yonezawa (material in cultivation at Harvard Forest, Petersham, Massachusetts; no voucher collected).
S. scilloidea	Mexico, Oaxaca, Ixtlán, *LaFrankie IV-21a.*
S. paniculata	Costa Rica, Cerro del Muerte, *LaFrankie IV-10c.*

anol series for complete extraction of soluble sugars and residues of decay, then vacuum infiltrated with 2 percent phloroglucinol in 95 percent ethanol and transferred directly to concentrated hydrochloric acid.

The living and preserved rhizomes of four other species of *Smilacina* were sectioned and stained in a manner similar to that described above. Living plants of these species were not experimentally treated, and development of the abscission zone was not studied directly; however, by examining the successively older scars found within a single rhizome, I could draw some inference concerning the later modification of the abscission zone. Voucher specimens have been deposited in the Gray Herbarium, Harvard University (GH) and are listed in TABLE 1.

RESULTS

SMILACINA RACEMOSA

The parenchyma and vascular bundles at the base of the aerial stem are not distinguishable from the surrounding tissue during the spring and summer (FIGURE 2). As individual stems begin to wither between July and October, a distinct abscission zone forms in the stem base at a scale-leaf internode 1–2 mm above the point of anatomical transition from the rhizome to the aerial stem (FIGURES 1, 3). The rhizome has an endodermis, amphivasal vascular bundles, and isodiametric parenchyma cells; the aerial stem lacks an endodermis but has a peripheral fibrous sheath, collateral vascular bundles, and elongated parenchyma cells. The position and appearance of the abscission zone is the same whether it occurs naturally or is induced.

The abscission zone consists of an outer suberized and lignified layer and an underlying layer of dividing cells that later also become suberized and lignified. The aerial stem usually separates from the rhizome just above the outer lignosuberized tissue, but there is no distinct separation layer, and often the dried stem remains weakly attached for a year or more.

Three stages can be recognized in the development of the abscission zone. In treated plants the first is seen seven days after cutting. (Plants collected zero and three days after cutting show no changes associated with abscission.) In

natural (i.e., untreated) plants this stage usually coincides with the first yellowing of the leaves, but the rate of development varies considerably from plant to plant. In the first stage the primary walls of the cortical parenchyma cells become suberized and partially lignified (FIGURE 4). The development of this ligno-suberized layer spreads inward to the center of the stem and outward until it includes the epidermis. The tracheids of most vascular bundles are water filled in fresh sections and are free of occlusions (FIGURE 5).

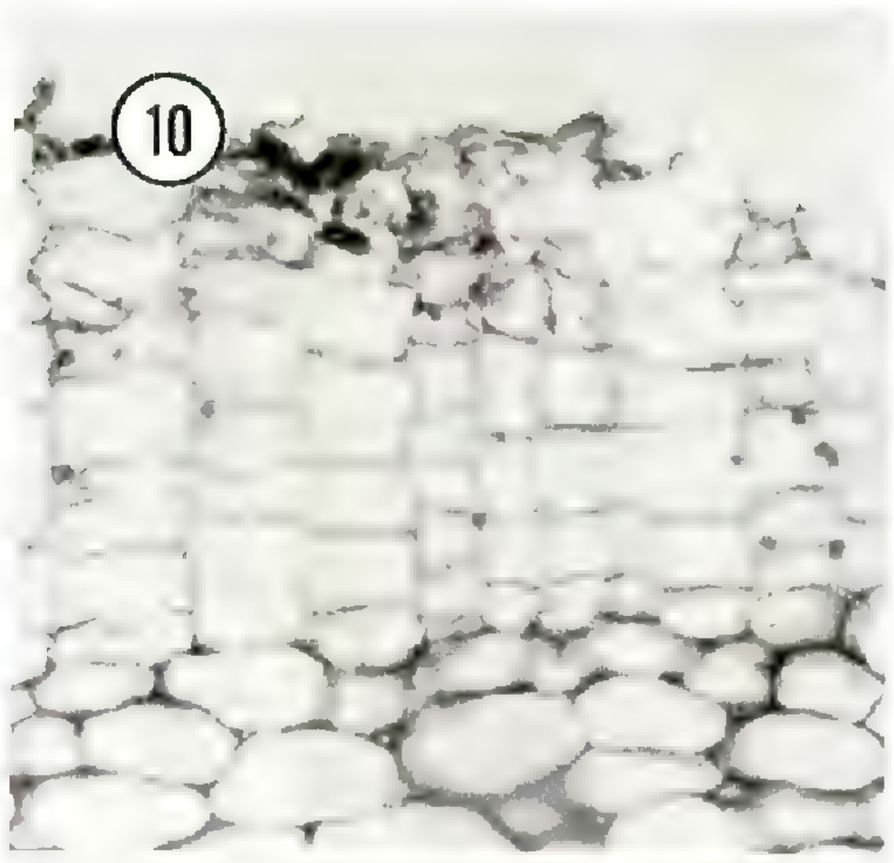
The second stage appears in treated plants 14 days after cutting; in untreated plants it is found when the entire aerial axis has turned yellow or retains only patches of green, and when at least a few leaves have dried and withered. This stage is characterized by an intensified lignin reaction, the occlusion of some of the xylem elements, and divisions within cells proximal to the ligno-suberized layer. The lumens of many tracheary elements are occluded with dark, amorphous contents (FIGURE 6), presumably gums or tannins, while other tracheary elements are air filled when examined in fresh sections. Cells immediately adjacent to the ligno-suberized layer repeatedly divide, with the new cell walls usually forming parallel to the plane of abscission. This results in subdivided cells (FIGURE 7). There is no evidence of a phellogen (i.e., permanently meristematic cells). At this stage the walls of the dividing cells are neither suberized nor lignified.

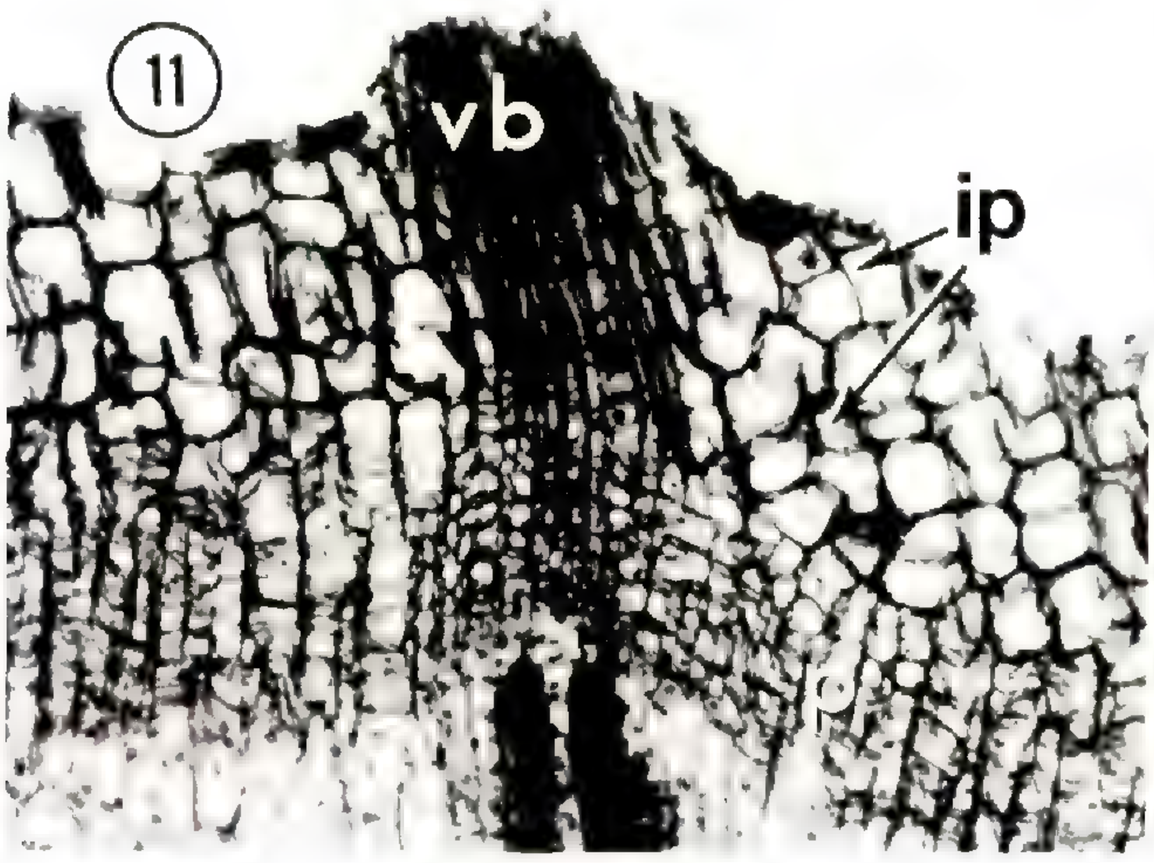
The third stage in stem abscission is first seen in the experimental plants 21 days after cutting but is found in untreated plants only when the main axis of the aerial shoot is dry and partially collapsed. In this stage the new walls of subdivided cells become suberized and lignified (FIGURE 8). No new cell divisions occur in adjacent cells. Xylem elements are completely occluded in all vascular bundles, and the occlusions extend 2 mm or more into the rhizome. In untreated plants the tissue distal to the ligno-suberized layer may decay, causing the withered aerial shoot to separate from the rhizome. Sometimes the weight of the terminal infructescence breaks the stem adjacent to the protective layer, but no mechanically weakened point or clear separation layer forms. As the aerial axis dries and withers, the ligno-suberized layer and the xylem occlusions become dark red-brown. The development of the protective layer is now complete; no further changes occur with age.

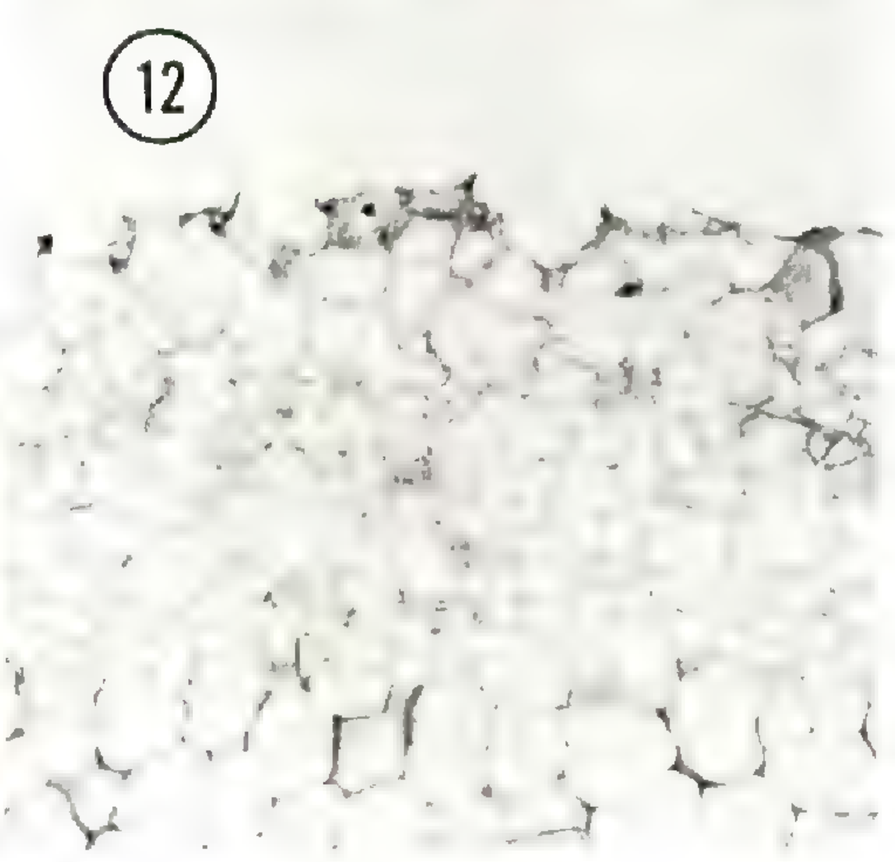
OTHER SPECIES OF SMILACINA

Two other species of *Smilacina* examined (*S. stellata, S. japonica*) have stem-abscission scars anatomically similar to those described for *S. racemosa*. There is a ligno-suberized layer of undivided and divided cells, beneath which occurs seemingly normal parenchyma.

Smilacina paniculata, an herb from montane cloud forests in Costa Rica, differs from the other species studied in the greater width of its aerial stem, and in that the rhizome of the renewal shoot swells to several times its initial diameter soon after the aerial axis emerges (FIGURE 9). Consequently, the abscission scar in *S. paniculata* is much larger than that found in any of the other species. The rhizome of *S. paniculata* is also distinct in that the epidermis is lost during the initial expansion of the rhizome, and a simple periderm subsequently develops on all of the exposed rhizome surfaces (FIGURE 10).







FIGURES 9–12. *Smilacina paniculata,* rhizome morphology and longitudinal sections. 9, rhizome viewed from above, × 0.2, showing scars of old shoots (arrow). 10, periderm of free rhizome surface, stained in safranin and alcian green, × 120. 11, stem base ca. 2 years after abscission of aerial shoot, stained in HCl-phloroglucinol, × 40; initial protective layer (ip) above, vascular bundle (vb) ruptured by periderm (p). 12, lower region of abscission zone, × 120, showing dividing parenchyma cells adjacent to periderm, × 100.

When the abscission zone of *Smilacina paniculata* first develops at the base of the aerial shoot, it is similar to that described for *S. racemosa* (i.e., a ligno-suberized layer of two or three cells). A few cell divisions occur in the parenchyma on the rhizome side of the ligno-suberized layer, and the resulting cells are subsequently incorporated into the protective layer. The tracheids of the vascular bundles are occluded several millimeters into the rhizome. These features characterize the protective region for approximately one year after the loss of the aerial shoot. In older portions of the rhizome, a thick periderm develops beneath the ligno-suberized layer (FIGURE 11), transecting the vascular bundles and augmenting the protective tissue of the abscission scar. The periderm of the abscission region joins with that of the free rhizome surface, but the two types of periderm can be distinguished by structural differences.

The periderm of the free rhizome surface consists of radial files of six or

seven cells that are uniform in size and shape, suggesting that they are derivatives of a phellogen, although this phellogen appears not to be permanent. When mature, all of the cells of the periderm are fully suberized and lignified and are quite distinct from the adjacent parenchyma. No cells occur in intermediate stages of development, which indicates that the periderm is not augmented through the continuous generation of new cells.

The periderm of the abscission region is thicker than that of the rhizome surface, it is not clearly demarcated from the adjacent parenchyma, and there is no indication of a phellogen. The mature periderm cells are varied in size and shape (FIGURE 12). Cell divisions seem to occur in parenchyma cells of progressively deeper levels, so that even when most of the periderm cells are suberized and lignified, parenchyma cells to the interior can be found dividing. Consequently, no clear line separates the periderm from the otherwise normal rhizome parenchyma.

The other tropical species examined, *Smilacina scilloidea,* is similar to *S. racemosa* and *S. stellata* in general morphology, but it develops a periderm on its free rhizome surface and in the abscission-scar region; the periderm is anatomically similar to that found in *S. paniculata.*

DISCUSSION

The abscission zone of *Smilacina* consists only of a protective layer that seals the parent stem; no discrete separation layer is formed. Such a situation may be characteristic of geophytes with sympodial rhizomes, but this generality can be supported only if many more species are examined.

The protective layer that seals the rhizome in *Smilacina racemosa* is notable for its early development, for the limited number of cells involved, and for its durability. In all but the last respect, the protective layer is similar to that found in the leaf-abscission zone of herbaceous dicotyledons. In plants such as *Phaseolus* and *Gossypium,* the initial protective layer forms when the cell walls of three or four layers of cells on the stem side of the separation layer become suberized and lignified. Tyloses occlude the vascular elements, and a few cell divisions occur adjacent to the ligno-suberized layer (Gawadi & Avery, 1950; Lee, 1911). Lee (1911) called these tissues the "initial protective layer" to distinguish them from a secondary protective layer that develops from a phellogen. It is quite remarkable that in *S. racemosa* such an initial protective region is able to seal the rhizome and remain intact for many years or even decades.

Many woody dicotyledons augment the initial protective layer with a periderm that develops some distance to the stem side of the abscission zone. Lee (1911) described the various ways in which this can occur, but typically a phellogen develops below the initial protective layer and establishes continuity with the periderm of the parent stem. In *Smilacina paniculata* the initial protective region is likewise augmented by a periderm, but a phellogen does not develop. Rather, the periderm is derived through the periclinal (and occasionally anticlinal) divisions of subjacent cells, and in this respect it more closely resembles the wound tissue of monocotyledons described by Swamy

and Sivaramakrishna (1972) than it does either the periderm found in the rhizome surface or the periderm described for other monocotyledons (Philipp, 1923). Admittedly, periderm tissue is poorly known in monocotyledons, and a better appreciation of the relationship of wound tissue to periderm tissue awaits their more careful comparative analysis. The protective region described for *Smilacina* can best be considered as an anticipatory wound response, establishing a water-tight seal prior to an actual break in the aerial axis.

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